

LIFE CYCLES OF MAYFLIES (EPHEMEROPTERA), WITH SPECIAL REFERENCE TO VOLTINISM

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ABSTRACT

This report is a survey in breadth of mayfly (Ephemeroptera) life cycles and includes data about 718 life cycles for 297 species. Most of the published reports are for Northern Hemisphere mayflies. About 60% of all mayfly life cycles were reported as univoltine, 30% multivoltine, 4% semivoltine, and 3% were judged variable, i.e. for a given population of a single report there would be different types of voltinism. In addition, for many species, different studies indicated different life cycle types. The survey indicates extensive flexibility of life cycles for many but not all mayfly species.

The univoltine winter cycle (single generation overwinters in the nymphal stage) is the most common single life cycle type. Baetid species, mainly Baetis, are mainly multivoltine. Ephemerellids, mainly Ephemerella, and heptageniid species are mainly univoltine, members of these two families accounting for more than half the univoltine cycles reported. Ephemerids, entirely Ephemera and Hexagenia, are the major semivoltine group. Cycles exhibiting a long period of egg dormancy, either in summer or winter, are common in mayflies; for example about 25% of all life cycles are summer cycles with a long period of egg dormancy in winter.

Yearly nymphal periodicity (or cohort production interval, CPI), an important factor in secondary production estimates, was calculated for species of all life cycle types. The average values for Northern Hemisphere mayflies of each life cycle are: 11.0 months for univoltine winter cycle (no summer egg-dormancy); 7.8 months for univoltine winter cycle with summer egg-dormancy; 4.1 months for univoltine summer cycles; and 23.8 months for the semivoltine cycles.

Each life cycle type has a characteristic seasonal reproductive period (equating reproductive period with adult periodicity). About half of all Northern Hemisphere mayflies reproduce in June and July. Multivoltine mayflies have the most extensive reproductive period and the semivoltine mayflies the most restrictive. Univoltine summer mayflies generally reproduce later in the year than univoltine winter mayflies. Possible adaptive strategies of these average reproductive periods are discussed.

Clear relationships between life cycle types and body size of individual species or phylogenetic position are not evident, but mayfly life cycle types may change predictably from the tropics to the arctic. Some features of flexible and rigid life cycles are discussed, as is importance of distinguishing cohorts from generations. Several areas of future research are suggested, especially the need for complete voltinism data of tropical mayflies.

Key words:

Ephemeroptera, mayflies, life cycles, voltinism, strategies, reproduction, production, literature.

RÉSUMÉ

Le rapport présente une reconnaissance complète des cycles biologiques des éphémères (Ephemeroptera); il contient des données sur 718 cycles biologiques appartenant à 218 espèces. La plupart de ces données proviennent d'espèces de l'hémisphère nord. Ces rapports ont indiqué qu'environ 60% de ces cycles sont univoltins, 30% multivoltins, 4% semivoltins, et que 3% sont variables, c'est à dire que pour une certaine population, un rapport a indiqué la présence de plusieurs types de voltinisme. De plus, pour un grand nombre d'espèces, différentes études ont rapporté différents types de cycle biologique, indiquant qu'il existe une grande souplesse, quant au type de cycle, chez un certain nombre d'espèces d'éphémères.

Le cycle univoltin hivernal (une génération hiberne à l'état de nymphe) est le type de cycle le plus courant. Les espèces de Baetidae (principalement Baetis) sont surtout multivoltines, tandis que les espèces d'Ephemerellidae (principalement Ephemerella) et d'Heptageniidae sont surtout univoltines, ces deux familles contenant plus de la moitié des cycles univoltins. Les Ephemeridae (toutes les espèces d'Ephemerella et d'Hexagenia) forment le groupe principal d'espèces semivoltines. Une longue période de dormance, à l'état d'oeuf, aussi bien en été qu'en hiver, est commune chez les éphémères: par exemple, environ 25% des cycles décrits sont des cycles estivaux avec une longue période de dormance hivernale.

La durée du stage nymphal (ou intervalle de production des cohortes), une importante donnée requise pour l'estimation de la production secondaire, a été calculée pour des espèces appartenant à tous les types de cycle biologiques. Les durées moyennes du stage nymphal des éphémères de l'hémisphère nord sont respectivement 11 mois pour les espèces univoltines hivernales (sans période de dormance estivale), 7.8 mois pour les espèces univoltines hivernales (avec période de dormance estivale), 4.1 mois pour les espèces univoltines estivales et 23.8 mois pour les espèces semivoltines.

Chaque type de cycle biologique à une saison de reproduction (qui est assimilée à la période d'apparition des adultes) qui lui est caractéristique. Près de la moitié des espèces d'éphémères de l'hémisphère nord se reproduisent en Juin et Juillet. Les périodes de reproduction les plus longues se trouvent parmi les espèces multivoltines tandis que les périodes les plus courtes se trouvent chez les espèces semivoltines. Les espèces univoltines estivales se reproduisent généralement plus tard que les espèces univoltines hivernales. La valeur adaptative de ces diverses longueurs de la période reproductive est examinée.

Il ne paraît pas y avoir de correspondance entre le type de cycle biologique et la taille, ou la position phylogénétique de chaque espèce; mais il semble que les cycles biologiques changent d'une façon prévisible des tropiques aux pôles. Certaines caractéristiques des cycles qui sont rigides, vis-à-vis de leurs pendant plus souples sont examinées ainsi que la nécessité de faire la distinction entre cohortes et générations. Plusieurs domaines de recherche future sont suggérés et l'importance d'obtenir des données sur le voltinisme des espèces tropicales est particulièrement notée.

Ephemeroptera, éphémères, cycles biologiques, voltinisme, stratégies, reproduction, production, revue.

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INTRODUCTION

Ephemeroptera, or mayflies, is a small but important order of aquatic insects. Twenty families of recent mayflies include slightly more than 200 genera and 2,000 species. Adult mayflies are unique among insects because there is usually an additional molt once the winged stage is achieved. Adults (the subimago and imago stages combined) seldom live for more than three days and do not feed. Most nymphs have, relative to most insect groups, a large and varied number of instars (from about 10 to 50 depending on the species). Most nymphs live only in unpolluted lakes and streams, where they sometimes occur in very large numbers (up to 10,000/m²); they can be an important component of secondary production generally and food for fish specifically. They have also been used as models for a variety of experimental aquatic studies. Unfortunately, accurate instar analysis of field populations is usually impossible, and this aspect of their way of life is usually missing in most life cycle studies.

The year 1957 might be considered a benchmark in study of mayfly life cycles; in that year T.T. Macan (1957b) reported on the life cycles of several British species and for each presented nymphal size frequency data throughout the life cycle. Since the 1950's, mayfly life cycle data have rapidly accumulated (Fig. 1), many of the studies being modelled after those of Macan. In the 1960's and 1970's, with the emphasis on computer-assisted quantitative studies of communities, descriptive life cycle studies did not receive high research priority. Although mayfly life cycle data continued to accumulate rapidly, often these data in reports of benthic studies were relegated to brief, observations, with no possibility of data interpretation by interested readers.

Presently, there is renewed interest in life cycles, as aquatic biologists realize the life cycle is an integral part of whole community processes and therefore often needed for interpreting these processes. In 1978, a symposium entirely devoted to life cycles and sponsored by the North American Benthological Society of America was held in Winnipeg, Canada (see Rosenberg

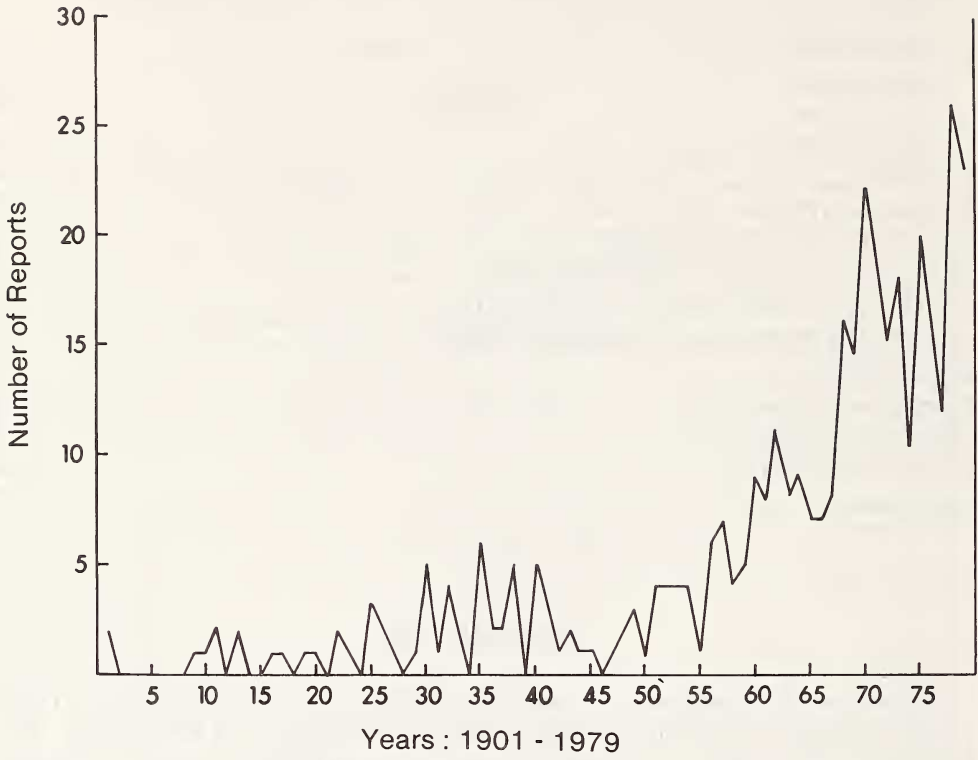


Figure 1. Number of published reports pertaining to mayfly life cycles, 1901-1979.

1979). Several workers pointed out the practical importance of life cycle data to aquatic research: sampling procedures for insects (Resh) and non-insects (Malley and Reynolds), taxonomy (Oliver), bioassays (Buikema and Benfield), pollution (Lehmkuhl) and food quality (Anderson and Cummins). In the symposium's summary, Waters called for a data bank of basic life cycle information and pointed out the importance of including features, e.g. voltinism, that might be expected under different environmental conditions. One result of this symposium was a review paper (Waters 1979) on how life cycles influence production estimates of benthic invertebrates.

Since 1965, my students and I have acquired complete life cycle data for 42 mayfly species of Alberta, Canada. Data on only about 40% of these cycles have as yet been published. Initially I had planned a life cycle synopsis of only the Alberta species; but an extensive survey of mayfly life cycles now seems in order, and the synopsis was expanded to include data about all mayfly life cycle reports that I could obtain.

A few key features, e.g. life span, growth, reproduction, when quantified in time, will each express information about the sum total of numerous biological processes and can be conveniently used to classify an organism's life cycle. The four criteria of mayfly life cycles considered in this survey follow those outlined by Tauber and Tauber (1978) for insects generally: egg dormancy, growth and development, reproduction, and dispersal, although dispersal was not treated in detail. Criteria were treated mainly from a phenological approach emphasizing voltinism of the various taxa. "Life cycle" and "life history" are used synonymously, although to some workers the terms have different meanings; e.g. systematists might prefer to restrict the term life history to connotations about evolutionary history of species.

The objectives were to (1) make available references about life cycles of the various mayfly taxa, (2) group and analyze life cycles using a voltinism classification scheme, and (3) discuss some of the mayfly life cycle types as they relate to interpretations of aquatic community processes and as they relate to adaptive strategies of mayflies.

METHODS

Literature Survey

About 400 papers were used in the survey. The survey stopped in October 1979; but I also included some published accounts of mayfly life cycles appearing later, especially those in the Proceedings of the Second and the Third International Conferences on Ephemeroptera. The following information was recorded for each species of each life cycle report: geographical location including latitude and, if pertinent, altitude, lentic or lotic study, type voltinism (see below), nymphal periodicity, adult periodicity, and egg stage duration. For many species egg duration was deduced from nymphal and adult periodicity. The species' life cycles were then grouped into one of two categories based on completeness of the study: (1) life cycle reports that always included data on voltinism and often information on growth, egg stage and adult periodicity; (2) reports pertaining only to adult periodicity (mainly emergence studies); this information was usually only recorded if the adult data were from routine sampling or observations throughout the adult stage of the population in question. Data of this second category were used only in the Reproduction Section.

Occasionally life cycles of a particular study were reported more than once. An attempt was made to use these cycles only once in the analysis (although all the literature citations were

Table 1. Total numbers and percentage of species having at least one cycle of the type in question and total number and percentage of life cycles reported for each type. See Methods for further explanation.

	Total Species		Total Life Cycles	
	No.	%	No.	%
Total Univoltine	218	73.4	455	63.3
U?	8	2.7	9	1.3
Uw	142	47.8	296	41.2
Us	80	26.9	141	19.6
Us-Uw	7	2.4	9	1.3
Total Multivoltine	109	36.7	217	30.2
M?	3	1.0	4	0.6
MB	64	21.5	144	20.1
MB?	5	1.7	4	0.6
MBss	19	6.4	26	3.6
MBws	49	16.4	114	15.9
MP	19	6.4	20	2.8
MB-MP	3	1.0	3	0.4
MNP	35	11.8	46	6.4
Total				
Uni-Multivoltine	7	2.4	7	1.0
Us-MBss	3	1.0	3	0.4
Uw-MBws	4	1.3	4	0.6
Total Semivoltine	12	4.0	28	3.9
2Y	12	4.0	26	3.6
3Y	1	0.3	1	0.1
2Y-3Y	1	0.3	1	0.1
Total				
Uni-Semivoltine	7	2.4	11	1.5
Uw-2Y	7	2.4	11	1.5
Totals	297		718	

included), but some redundancy undoubtedly exists. Another problem pertains to taxonomic treatment. Several taxonomic revisions have been published during and after the survey. It was not possible to incorporate all of these into the survey, but their omission should have little bearing on the analysis. Except for using the recent *Baetis* revision of Morihara and

McCafferty (1979) and *Ephemerella* revision of Allen (1980), names follow Edmunds *et al.* (1976) for North American species, Puthz (1978) for European species; and for the few species reported from other areas the nomenclature of the article in question was used.

Life Cycle Types

The classification scheme used here implies a degree of rigidity for mayfly life cycles that for many species (as will be discussed later) is probably not justified. Nevertheless, some sort of classification is necessary as a first step in reducing the complexities of mayfly life cycle features to an orderly system. I chose a voltinism scheme because most mayfly life cycles have been reported in terms of generations per year. An alternate system is to separate annual cycle into non-seasonal and seasonal cycles, with the seasonal cycle being further divided into slow seasonal and fast seasonal cycles (Hynes 1961). One advantage here is that generations and cohorts do not always have to be distinguished. Unfortunately, not enough mayfly life cycles have as yet been described in terms of fast and slow cycles to make the scheme applicable for a global survey.

The major categories (see for example Table 1), univoltine, multivoltine and semivoltine, need no explanation. The greatest degree of certainty in accurately interpreting the life cycle is implied by the major voltinism types, and much of the analysis and discussion is based only on major categories. Each of these three major life cycle types (plus two additional major types, see below) was separated into more specific life cycle categories based in part on Landa's (1968) classification system. These subtypes are more subjective, but compilations based only on major voltinism features could conceal important life cycle differences. Life cycle types are defined as follows:

Univoltine.

- U? - a seasonal univoltine cycle; but the report does not indicate what type.
- Uw - seasonal univoltine winter cycle; the population overwinters in the nymphal stage.
- Us - seasonal univoltine summer cycle; hatching, growth and emergence take place in summer; the population overwinters in the egg stage.
- Us-Uw - a seasonal univoltine cycle where most of the new generation overwinters in the egg stage, but a small part of the population overwinters in the nymphal stage.

Multivoltine.

- M? - seasonal multivoltine cycle, but the report does not indicate what type; the few reports of three generations in two years were also placed in this type.
- MB - the total number of seasonal bivoltine cycles.
- MB? - a seasonal bivoltine cycle, but the report does not indicate whether there are two summer generations or a summer and a winter generation.
- MBss - seasonal bivoltine summer cycle; following summer generations, the population overwinters in the egg stage.
- MBws - seasonal bivoltine winter-summer cycle. There is an overwintering generation in the nymphal stage and one summer generation.

MP - the total number of seasonal polyvoltine cycles where there are three or more generations a year, usually consisting of two or more summer generations and an overwintering generation in the nymphal stage. Throughout, polyvoltine refers only to three or more generations a year, though polyvoltine usually means the same thing as multivoltine. Using polyvoltine in this sense is more convenient than constantly saying "trivoltine or greater" when contrasting these multivoltine cycles with the bivoltine cycles.

MB-MP

- a seasonal multivoltine cycle where the population of a given study might be bivoltine or polyvoltine depending on year, local habitat, or in some taxa partly bivoltine and partly polyvoltine from the same egg cohort.

MNP - non-seasonal polyvoltine cycle. These reports are from tropical and semitropical regions; for many, polyvoltinism was inferred from emergence data if there were few observations of other life stages.

Total Uni-Multivoltine.

This major category and the Total Uni-Semivoltine category are the variable life cycle types and include species whose life cycles (of a given report) vary between major types of voltinism.

Us-MBss

- a seasonal variable cycle, where the report indicates one or two summer generations, depending on year, local habitat, or even from a single egg cohort.

Uw-MBws

- a seasonal variable cycle where the report indicates the population typically has a univoltine winter cycle; but, depending on year, local habitat or even from a single egg cohort, there occasionally might also be a summer generation.

Total Semivoltine.

2Y - seasonal semivoltine cycle with a generation time of about two years (closer to two years than one year).

3Y - seasonal semivoltine cycle with a generation time closer to three years than two years.

2Y-3Y

- seasonal semivoltine cycle where the report indicates one generation in two or three years, depending on year, local conditions, or even from a single egg cohort.

Total Uni-Semivoltine

Uw-2Y

- a seasonal variable cycle where the report indicates either a univoltine winter cycle or a two-year semivoltine cycle, depending on year, local habitat or from a single egg cohort.

Explanation of Tabular Summary Tables

Tabular summaries for each family and genus have six columns. Meaning of column headings and significance of their values should be clear by working through an example, i.e. Table 2, Baetidae.

Column 1 (Species No.). – Adequate voltinism data were available for 58 species of Baetidae; 13 species of Baetidae had *at least one* Us (univoltine summer) cycle, etc. Thus, some subtotals add to more than total number because some species were reported with more than one life cycle type.

Column 2 (% Species in Family). – 22.4% of all Baetidae species had *at least one* Us cycle, etc. For reasons given for column 1, the subtotal percentages do not necessarily add to 100.

Column 3 (% All Species--with that life cycle type). – Baetid species accounted for 16.3% of all mayfly species having a Us cycle.

Column 4 (No. of Life Cycles). – The 58 species of Baetidae accounted for a total of 183 reported life cycles; 23 of Baetidae life cycles were reported as Us. Here, subtotals of major voltinism types add to 183.

Column 5 (% Life Cycles in Family). – 12.6% of all Baetidae life cycles were Us.

Column 6 (% All Life Cycles--of that life cycle type). – Baetidae life cycles accounted for 16.3% of all life cycles reported as Us.

Tabular summaries are given for most families and for species having at least five life cycle reports. Lists of all species, their literature citations, and “consensus” life cycle types are given in the appendix.

GENERAL ANALYSIS

The survey consisted of 718 life cycles for 297 mayfly species (Table 1). The totals are 1,474 items of life cycle information for 490 species with inclusion of data pertaining strictly to adult periodicity.

Baetidae

Values for this family constituted 25% of all mayfly life cycles reported. Generally, members of this widely distributed family exhibit seasonal multivoltine cycles (Table 2). Only a few baetid species exhibit the most common mayfly life cycle type, the univoltine winter cycle.

Baetis Leach

Substantially more life cycles were reported for *Baetis* than for any other mayfly genus. Populations of the 32 species with adequate voltinism data are mainly multivoltine (Table 3). *Baetis* species account for most of the exclusively summer (Us, MBss, Us-Mbss) life cycle types. *Baetis* populations had few univoltine winter cycles.

Number of life cycle reports for *B. rhodani* populations was second only to the number reported for *Ephemerella ignita* (Table 4). Throughout its range, *B. rhodani* populations appear to have consistently a seasonal bivoltine cycle with an overwintering generation in the nymphal stage and one summer generation. Sometimes, however, there can be a second summer generation, for example in the Atlantic Pyrenees of France (Thibault 1971b, Benech 1972, Neveu *et al.* 1979). In many areas, *B. rhodani* adults are found continuously throughout the summer, and several workers reporting a bivoltine cycle suggest the possibility of additional

Table 2. Baetidae tabular summary. Number and percentage of species having at least one cycle of the type in question in family and number and percentage of life cycles reported for each type. See Methods for further explanation.

	Species			Life Cycles		
	<i>No.</i>	<i>% Fam.</i>	<i>% All</i>	<i>No.</i>	<i>% Fam.</i>	<i>% All</i>
Total Univoltine	18	25.9	8.3	40	21.9	8.8
Uw	6	10.3	4.2	17	9.3	5.7
Us	13	22.4	16.3	23	12.6	16.3
Total						
Multivoltine	54	93.1	49.5	141	77.0	65.0
M?	1	1.7	33.3	2	1.1	50.0
MB	36	62.1	56.3	104	56.8	72.2
MB?	2	3.4	40.0	2	1.1	50.0
MBss	16	27.6	84.2	23	12.6	88.5
MBws	25	43.1	51.0	79	43.2	69.3
MP	13	22.4	68.4	14	7.7	70.0
MB-MP	2	3.4	66.7	2	1.1	66.7
MNP	15	25.9	42.9	19	10.4	41.3
Total Uni-						
Multivoltine	2	3.4	28.6	2	1.1	28.6
Uw-MBws	2	3.4	50.0	2	1.1	50.0
Totals	58			183		

Table 3. Tabular summaries: *Baetis* and *Ephemerella*. Number and percentage of species having at least one cycle of the type in question in genus and number and percentage of life cycles reported for each type.

	Species			Life Cycle		
	No.	% Gen.	% All	No.	% Gen.	% All
<i>Baetis</i>						
Total Univoltine	13	40.6	6.0	25	22.1	5.5
Uw	3	9.4	2.1	6	5.3	2.0
Us	10	31.3	12.5	19	16.8	13.5
Total						
Multivoltine	28	87.5	25.7	87	77.0	40.1
MB	26	81.3	40.6	74	65.5	51.4
MBss	10	31.3	52.6	15	13.3	57.7
MBws	19	59.4	38.8	59	52.2	51.8
MP	8	25.0	42.1	9	8.0	45.0
MB-MP	1	3.1	33.3	1	0.9	33.3
MNP	2	6.3	5.7	3	2.7	6.5
Total Uni-						
Multivoltine	1	3.1	14.3	1	0.9	14.3
Uw-MBws	1	3.1	25.0	1	0.9	25.0
Totals	32			113		
<i>Ephemerella</i>						
Total Univoltine	19	95.0	8.7	84	95.5	18.5
U?	2	10.0	25.0	3	3.4	33.3
Uw	14	70.0	9.9	43	48.9	14.5
Us	6	30.0	7.5	36	40.9	25.5
Us-Uw	1	5.0	14.3	2	2.3	22.2
Total						
Multivoltine	2	10.0	1.8	3	3.4	1.4
MB	2	10.0	3.1	3	3.4	2.1
MBws	2	10.0	4.1	3	3.4	2.6
Total Uni-						
Multivoltine	1	5.0	14.3	1	1.1	14.3
Us-MBss	1	5.0	25.0	1	1.1	25.0
Totals	20			88		

Table 4. Number of life cycles of each type reported for (1) *Baetis rhodani*, (2) *B. alpinus*, (3) *B. muticus*, (4) *B. vernus*, (5) *B. scambus*, (6) *B. fuscatus*, (7) *B. tricaudatus*, and (8) *Centroptilum luteolum*.

	1	2	3	4	5	6	7	8
Total								
Univoltine	3	2	1	2	4	1	—	—
Uw	3	2	—	—	—	—	—	—
Us	—	—	1	2	4	1	—	—
Total								
Multivoltine	24	5	7	4	4	6	7	9
MB	20	5	6	4	4	5	5	8
MBss	1	—	—	1	2	5	—	—
MBws	19	5	6	3	2	—	5	8
MP	3	—	1	—	—	1	2	1
MB-MP	1	—	—	—	—	—	—	—
Total Uni-								
Multivoltine	—	—	—	1	—	—	—	—
Uw-MBws	—	—	—	1	—	—	—	—
Totals	27	7	8	7	8	7	7	8

summer generations. Humpesch (1979b) distinguished 10 *B. rhodani* cohorts over 30 months in an Austrian population; although cohorts should not be confused with generations, this perhaps suggests a seasonal polyvoltine species, with absolute number of generations varying from year to year.

Baetis rhodani populations with univoltine winter cycles have been reported from the far north, above latitude 65°N (Ulfstrand 1968), but also from upland areas at lower latitudes, i.e. Germany (Illies 1952) and Poland (Sowa 1965). Most of *Baetis* species of the far north, e.g. *B. macani macani* in Europe and *B. macani bundyae* (see Appendix for all species not included in the tables) in North America, exhibit summer cycles, but there are apparently no reports of exclusively summer cycles for *B. rhodani* populations at high latitudes. There is one report of a summer cycle, i.e. two summer generations, for *B. rhodani* from Austria (Pleskot 1961).

Populations of the Palearctic *B. alpinus*, *B. muticus* and *B. vernus* exhibit one of several life cycle types, although they are mainly bivoltine with a nymphal winter generation (Table 4); in contrast *B. scambus* and *B. fuscatus*, also Palearctic species, are mainly summer species. Life cycle reports for the North American *B. tricaudatus* (including *B. vagans*) indicate only multivoltine cycles, populations having either an MBws bivoltine cycle or a seasonal polyvoltine

cycle with one overwintering nymphal generation and two or more (although the exact number often appears to be speculative) summer generations.

Cloeon Leach

Cloeon species exhibit a variety of life cycle types; and, in contrast to *Baetis* populations, the life cycle types are fairly evenly distributed between univoltine winter cycles, bivoltine cycles, seasonal polyvoltine cycles, and the variable uni-multivoltine type. Few exclusively summer cycles were reported for *Cloeon*.

Two species, *C. dipterum* and *C. simile*, account for most of *Cloeon* life cycles (Table 7). The mainly Palearctic *C. dipterum* (it has been reported once from North America, Traver 1962) has no uniform life cycle type; in fact, populations apparently are very flexible in their life cycles, often exhibiting univoltine winter cycles, occasionally bivoltine cycles, and sometimes a single population is partly univoltine and partly bivoltine (a uni-multivoltine life cycle type). *Cloeon dipterum* populations are ovoviviparous, at least in part of the species' range, but how this might be related to the flexible voltinism of this species is obscure. Certainly, ovoviviparity would account for the absence of exclusively summer cycles in *C. dipterum*. The non-ovoviviparous *C. simile* has been reported as having a summer cycle; but generally, as for *C. dipterum*, populations appear to be quite flexible, having either univoltine or multivoltine cycles, presumably depending on environmental factors.

Other Baetid Genera

The *Centroptilum* species with adequate voltinism data are mainly multivoltine, with a relatively large proportion of the species having at least one bivoltine summer-summer cycle. The Palearctic *C. luteolum*, the most reported *Centroptilum* species, apparently always features an overwintering nymphal population, most of the life cycle being reported as the bivoltine winter-summer cycle (Table 4). However, there is some dispute, at least for certain areas, whether the cycle is bivoltine or univoltine with an extended period of emergence (see Bretschko 1965, Macan and Maudsley 1968, Lavandier and Dumas 1971, and Brittain 1974).

Populations of *Pseudocloeon* are mainly multivoltine, with a large proportion of seasonal polyvoltine cycles. The two species of *Procloeon* with voltinism data, *P. bifidum* (Table 7) and *P. ornatum*, are mainly summer species, with two summer generations. The remaining baetid genera for which there were voltinism data, *Callibaetis*, *Baetiella* and *Baetodes* (see appendix), exhibit multivoltine cycles.

In short, members of this important mayfly family exhibit a variety of life cycle types, with a tendency for multivoltine cycles and also flexibility in life cycle types. Species of Baetidae, especially *Baetis* species, are consistently important in numerical abundance studies (Clifford 1980), and perhaps this dominance in numerical abundance is accounted for in part by the plasticity in their life cycle features.

Caenidae

Life cycle reports for Caenidae made up about 5% of all mayfly life cycle reports. At the family level, there was no consistent life cycle type, about half the cycles being univoltine and half being multivoltine (Table 5).

Most life cycles of Caenidae were those of *Caenis* species. About half the *Caenis* cycles are univoltine, mainly univoltine winter, and about half are multivoltine, mainly the bivoltine

Table 5. Caenidae and Oligoneuriidae tabular summaries.

	Species			Life Cycles		
	<i>No.</i>	<i>% Fam.</i>	<i>% All</i>	<i>No.</i>	<i>% Fam.</i>	<i>% All</i>
Caenidae						
Total Univoltine	14	73.7	6.4	21	58.3	4.6
U?	3	15.8	37.5	3	8.3	33.3
Uw	7	36.8	4.9	12	33.3	4.1
Us	5	26.3	6.3	6	16.7	4.3
Total						
Multivoltine	11	57.9	10.1	15	41.7	6.9
MB	8	42.1	12.5	11	30.6	7.6
MB?	1	5.3	20.0	1	2.8	25.0
MBss	1	5.3	5.3	1	2.8	3.9
MBws	6	31.6	12.2	9	25.0	7.9
MB-MP	1	5.3	33.3	1	2.8	33.3
MNP	3	15.8	8.6	3	8.3	6.5
Total Uni-						
Multivoltine	1	5.3	14.3	1	2.8	14.3
Us-MBss	1	5.3	25.0	1	2.8	25.0
Totals	19			36		
Oligoneuriidae						
Total Univoltine	9	100.0	4.1	12	100.0	2.6
Uw	1	11.1	0.7	1	8.3	0.3
Us	8	88.9	10.0	11	91.7	7.8
Totals	9			12		

Table 6. Ephemerellidae tabular summary.

	Species			Life Cycles		
	No.	% Fam.	% All	No.	% Fam.	% All
Total Univoltine	33	94.3	15.1	107	94.7	23.5
U?	2	5.7	25.0	3	2.7	33.3
Uw	25	71.4	17.6	61	54.0	20.6
Us	9	25.7	11.3	41	36.3	29.1
Us-Uw	1	2.9	14.3	2	1.8	22.2
Total Multivoltine	3	8.6	2.8	4	3.5	1.8
MB	2	5.7	3.1	3	2.7	2.1
MBws	2	5.7	4.1	3	2.7	2.6
MNP	1	2.9	2.9	1	0.9	2.2
Total Uni- Multivoltine	1	2.9	14.3	1	0.9	14.3
Us-MBss	1	2.9	33.3	1	0.9	33.3
Total Semivoltine	1	2.9	8.3	1	0.9	3.6
2Y	1	2.9	8.3	1	0.9	3.9
Totals	35			113		

winter-summer cycle. Even at the species level, i.e. *C. horaria*, both univoltine and multivoltine cycles have been reported (Table 7). In short, as was found for many of the baetids, life cycle types of many *Caenis* populations seem quite flexible. In contrast, *Brachycercus* populations appear to exhibit mainly univoltine summer cycles; species of *Brachycercus* accounted for four of six univoltine summer cycles of Caenidae.

Ephemerellidae

Generally, ephemerellid species exhibit univoltine cycles, with more winter cycles than summer cycles (Table 6). Collectively, ephemerellid and heptageniid populations account for about half the univoltine cycles.

Table 7. Number of life cycles of each type reported for (1) *Cloeon dipterum*, (2) *C. simile*, (3) *Procloeon bifidum*, (4) *Caenis horaria*, (5) *Ephemerella ignita*, (6) *E. aurivillii*, (7) *E. mucronata*, and (8) *Torleya major*.

	1	2	3	4	5	6	7	8
Total								
Univoltine	9	2	—	3	42	5	7	5
Uw	9	1	—	3	10	5	6	5
Us	—	1	—	—	30	—	1	—
Us-Uw	—	—	—	—	2	—	—	—
Total								
Multivoltine	8	3	5	2	2	—	—	—
MB	6	3	4	1	2	—	—	—
MB?	—	—	1	1	—	—	—	—
MBss	—	—	2	—	—	—	—	—
MBws	6	3	1	—	2	—	—	—
MP	1	—	1	—	—	—	—	—
MB-MP	—	—	—	1	—	—	—	—
MNP	1	—	—	—	—	—	—	—
Total Uni-								
Multivoltine	1	—	—	—	1	—	—	—
Us-MBss	—	—	—	—	1	—	—	—
Uw-MBws	1	—	—	—	—	—	—	—
Totals	18	5	5	5	45	5	7	5

***Ephemerella* (sensu stricto, see Allen 1980)**

Ephemerella species account for most life cycle reports (Table 3) of Ephemerellidae. *Ephemerella* populations exhibit mainly univoltine cycles. The large number of summer cycles reported is due mainly to numerous life cycles reported for *E. ignita*, this species accounting for more than half of all *Ephemerella* life cycle reports (Table 7). There were more life cycle reports for *E. ignita* than any other mayfly species. Populations of this Palearctic species exhibit mainly univoltine summer cycles, but there were reports of univoltine winter cycles, bivoltine winter-summer cycles, and even cycles (Us-Uw) where part of the population overwinters in the egg stage and part in the nymphal stage. Elliott (1978) surveyed many life cycle reports for *E. ignita* through 1977; he states the cycle in upland streams of Europe is mainly the univoltine summer cycle; whereas in various lowland European streams, nymphs have been found throughout the winter. The complex relationship between water temperature

and hatching time of eggs of *E. ignita* has been studied in the laboratory by Bohle (1972) and Elliott (1978). In a field study, Neveu *et al.* (1979) confirmed Elliott's results. In contrast to *E. ignita*, *E. aurivillii* and *E. mucronata* populations generally have straight-forward univoltine winter cycles.

A variation of the univoltine winter cycle occurs when the population spends much of the summer in some sort of egg dormancy state. As discussed later, this type of univoltine winter cycle, which might be considered opposite of the univoltine summer cycle (where egg stage dormancy occurs in winter), is probably commoner than would be indicated by publication about life cycles. Of 15 species judged to have at least 4 months of egg dormancy in summer, five were *Ephemerella* species.

Other ephemereid genera

Eurylophella and *Drunella* populations have mainly univoltine winter cycles. However, *Eurylophella funeralis* had a 2-year cycle in a northeastern USA stream (Fiance 1978). This appears to be the only record, based on adequate life cycle data, of an ephemereid having a semivoltine cycle. *Serratella* species have been reported exhibiting either univoltine winter or univoltine summer cycles. *Torleya major* (= *T. belgica*) populations were exclusively univoltine winter (Table 7). The one life cycle reported for the tropical *Teloganodes* indicates a non-seasonal life cycle with emergence throughout the year.

Ephemeridae

This is the major family of semivoltine mayflies, accounting for 58% of the species having exclusively semivoltine cycles and 82% of all the exclusively semivoltine cycles. Species of *Ephemera* and *Hexagenia* account for all the ephemerid life cycles reported (Table 8).

Ephemera Walsh

Most *Ephemera* life cycles were reported as semivoltine; however four of the six species exhibit at least one univoltine cycle. Two species, *E. danica* and *E. simulans*, account for most of *Ephemera* life cycle reports (Table 14). Populations of the Palearctic *E. danica* were reported as having univoltine winter cycles, semivoltine cycles, and sometimes with both univoltine and semivoltine cycles (Uw-2Y). Although other workers have alluded to a 3-year cycle for ephemerids, or other mayflies, e.g. *Palingenia*, the studies of Illies (1952) and Svensson (1977) are the most convincing of a definite three-year cycle. Svensson found for an *E. danica* population in Sweden that part of the population required two years to complete the cycle, whereas the other part took three years; at any one time as many as five generations were present. In contrast, Thibault (1971b), for an *E. danica* population of the French Pyrenees, found that from a single egg cohort, depending on hatching time, part of the population required one year to complete the cycle and part required two years. Whelan (1980) also reported a flexible, one- or two-year cycle for *E. danica* in Ireland. And Landa (1968) reported *E. danica* to have two generations in three years in central Europe. Clearly, this thoroughly studied species has a very flexible life cycle.

Life cycle reports for *E. simulans* indicate populations having either univoltine winter cycles or two-year cycles. There were neither variable cycles (i.e. both univoltine and semivoltine cycles from the same population) nor three-year cycles reported for *E. simulans*.

Hexagenia Walsh

Relatively fewer univoltine cycles were reported for populations of the Nearctic *Hexagenia* than for *Ephemera* (Table 8). Two species, *H. limbata* and *H. bilineata*, account for most of the *Hexagenia* life cycle reports (Table 14). Populations of *H. limbata* (not including the subspecies *occulata* and *viridescens*) were reported as having univoltine cycles, semivoltine cycles, and occasionally within a single population, depending on hatching time of the single egg cohort, part of the population completed the life cycle in one year and part required two years. Possibly there is a tendency for two year cycles for northern populations and one year cycles for southern populations (Swanson 1967); but other workers, e.g. Rutter and Wissing (1975), suggest that given the proper local conditions, especially water temperature, probably most *H. limbata* populations can exhibit either one- or two-year cycles or sometimes both cycles. In most taxa with both a one-year and two-year component to the cycle, most of the population exhibits the two-year cycle (Hudson and Swanson 1972, Rutter and Wissing 1975). Flannagan (1979) reported two life cycle types for *H. limbata* populations of Lake Winnipeg, Canada: one type featured a 14-month life span alternating with a 22-month life span; and the other was the typical two-year cycle. Obviously *H. limbata* populations have flexible life cycles, although three-year cycles have not been reported. In fact, Hunt (1953), for a Michigan, USA, population, obtained evidence based on water temperature data, that the maximum life span would probably have to be less than three years.

Hexagenia bilineata is mainly univoltine, though Fremling (1973a) obtained evidence for a quick summer generation as well as a winter generation. Certainly laboratory studies of nymphal growth suggest that rapid generations are possible for *H. bilineata* (Thomforde and Fremling 1968). In contrast, part of a population in a Nebraska, USA, reservoir required two years to complete the cycle (Hudson and Swanson 1972). Hence there can be an extraordinary variation in the life span of this mayfly, from about four to 24 months.

Heptageniidae

Complete voltinism data were available for more heptageniid species than for species of any other family. Heptageniid species exhibit mainly univoltine cycles (Table 9). Of 85 species for which there were voltinism data, more than 90% had at least one univoltine cycle. Because of the large number of species, it is difficult to generalize further at the family level.

Rhithrogena Eaton

Unlike most other major mayfly families, no single genus of Heptageniidae accounted for a disproportional large number of life cycle reports. *Rhithrogena* and *Ecdyonurus* populations comprise the largest number reports of life cycles for heptageniids. *Rhithrogena* species are mainly univoltine, all species for which there were adequate voltinism data having at least one univoltine cycle, most being univoltine winter cycles. Sowa (1975a) found a *R. loyaleae* population of the Carpathian Mountains, Poland, to be either univoltine or semivoltine depending upon water temperature. *Rhithrogena semicolorata* was the most reported heptageniid species (Table 10). Populations of the Palearctic species exhibit almost exclusively univoltine winter cycles; although Thibault (1971b) found a partial second generation (MBws) for *R. semicolorata* (and *Rithrogena iridina picteti*) in some streams in the French Pyrenees. Neveu *et al.* (1979) also reported a bivoltine winter-summer cycle for *R. diaphana* in the French Pyrenees.

***Ecdyonurus* Eaton**

In contrast to *Rhithrogena*, *Ecdyonurus* populations, although mainly exhibiting univoltine cycles, were reported having a relatively large number of bivoltine (MBws) cycles. Life cycle reports for *E. venosus* indicate populations having either univoltine or multivoltine cycles, but apparently not exclusively summer cycles (Table 10). *Ecdyonurus torrentis* and *E. lateralis* (= *Heptagenia lateralis*) are almost exclusively univoltine winter species. *Ecdyonurus dispar* and *E. submontanus* have often been reported having summer cycles.

Wise (1980) summarizes ecdyonurid life cycle reports of Great Britain. Humpesch (1980) gives data on hatching time of five *Ecdyonurus* species and comments on how such information is essential for distinguishing cohorts and hence accurately interpreting the life cycle. For example his data indicate no evidence of an obligatory egg diapause in *E. dispar*, despite populations usually being reported as having summer cycles.

***Heptagenia* Walsh**

Heptagenia populations exhibit a variety of life cycle types, most being univoltine winter cycles. Landa (1968) reported *H. sulphurea* (Table 10) populations of central Europe to have a summer generation in some years, and Ulfstrand (1968) reported populations of *H. dalecarlica* in Swedish Lapland (66°N) to be either univoltine or semivoltine, depending on locality. He also reported that, depending on hatching time, part of a *H. sulphurea* population could be univoltine and the other part semivoltine, with the semivoltine component of the population spending a year in the egg stage.

Other genera of Heptageniidae

Populations of both *Epeorus* and *Stenonema* exhibit mainly univoltine winter cycles, although several *Epeorus* species and *Stenonema tripunctatum* (Table 10) were also reported having bivoltine (MBws) cycles. Lehmkuhl (1968) and Richardson and Tarter (1976) summarize life cycle data for some North American *Epeorus* and *Stenonema* species respectively.

Populations of *Stenacron interpunctatum* (including all subspecies) exhibit several life cycle types and give no indication of a characteristic type (Table 10). Of all subspecies, *S. interpunctatum canadense* was the only one exhibiting univoltine cycles. McCafferty and Huff (1978) report a complex life cycle for *S. interpunctatum*, with part of the population contributing to three generations in two years, and the other part having one generation a year. McCafferty and Huff suggest potential for genetic mixing between generations because of differential growth among generations. The great variability in life cycles of *S. interpunctatum* might indicate two or more valid species within this group.

Cinygmula, *Cinygma* and *Ironodes nitidus* (= *Epeorus nitidus*) populations exhibit exclusively univoltine winter cycles. *Arthroplea*, *Macdunnoa*, *Anepeorus*, and *Pseudiron* populations apparently have only univoltine summer cycles. *Afronurus* and *Thalerosphyrus* are tropical mayflies, and the few available data, mainly adult periodicity records, indicate non-seasonal and presumably polyvoltine cycles.

Leptophlebiidae

Many leptophlebiids are tropical and this accounts for relatively large number of non-seasonal cycles reported for this family (Table 11). There are few variable-type life cycles

among the leptophlebiids. At the family level, a majority of life cycles are univoltine, due mainly to a few abundant temperate species.

***Paraleptophlebia* Lestage and *Leptophlebia* Westwood**

Generally, *Paraleptophlebia* populations are characterized as univoltine, having either winter or summer cycles. All *Paraleptophlebia* species have at least one univoltine cycle. Populations of the abundant Palearctic *P. submarginata* exhibit only univoltine winter cycles (Table 12). In contrast, the life cycle of the Nearctic *P. debilis* appears more flexible (Table 12). In a brown-water stream of Alberta, Canada, *P. debilis* invariably exhibits univoltine summer cycles, the nymphs appearing, growing, and emerging in about three months, June through August (Clifford 1969). Further south, in western Oregon, USA, the nymphal population is in the stream from about March through October (Lehmkuhl and Anderson 1971). And in New York State, USA, Gordon (1933) believed there were three generations in two years; this implies a nymphal population during some or all the winter months.

Life cycle data indicate *Leptophlebia* to be almost exclusively a univoltine taxon, but these data represent only a few abundant temperate species. Populations of the Palearctic *L. vespertina* and *L. marginata* have only univoltine winter cycles (Table 12). The eight cycles for *L. vespertina* populations represent one of the largest number of life cycles reported for a single species in which there was no deviation from a single life cycle type. Even at high latitudes, i.e. 61°N, populations of both *L. vespertina* and *L. marginata* are univoltine with invariably an overwintering nymphal population (Brittain 1978). The Nearctic *L. cupida* occurs over much of North America, from at least 35°N to 60°N, and has been studied over several years in Alberta, Canada (Clifford *et al.* 1979). Life cycle features of *L. cupida* have been reported from other North American areas as well. There is no indication of *L. cupida* populations deviating from a univoltine winter cycle, although emergence is progressively later at higher latitudes in North America (Clifford *et al.* 1979).

***Habrophlebia* Eaton, *Habroleptoides* Schoenemund and *Choroterpes* Eaton**

Populations of *Habrophlebia*, mostly *H. lauta*, have mainly univoltine winter cycles (Table 12). *Habroleptoides modesta* is apparently an entirely univoltine winter species. In contrast, reports for *Choroterpes* species indicate both univoltine and multivoltine cycles, the univoltine cycles being exclusively summer cycles. In Texas, USA, *C. mexicanus* is a seasonal polyvoltine species, having three overlapping generations a year (McClure and Stewart 1976).

Other genera of Leptophlebiidae

Atalophlebiodes (= *Deleatidium*) sp. or spp. from New Zealand apparently can have either univoltine winter or bivoltine cycles (Winterbourn 1974, 1978). The one life cycle report for *Traverella americana* indicates a univoltine summer cycle for this Nearctic species. The other leptophlebiids for which there were some life cycle data are tropical mayflies; and the cycles, based mainly on adult periodicity data, appear to be non-seasonal.

Metretopodidae

Few life cycle data are available for the two genera of this small family. For the Nearctic *Siphoplecton*, a life cycle study of a *S. basale* population from Alberta, Canada, indicates a straightforward univoltine winter cycle (Clifford 1976). Populations of *S. speciosum* in Florida,

USA are apparently non-seasonal (Berner 1950), although emergence data of Pescador and Peters (1974) might indicate a seasonal cycle for *S. speciosum* populations in certain areas of northern Florida. A recent life cycle study of a *Metretopus borealis* population in a northern Alberta, Canada, stream indicates a univoltine winter cycle (unpublished data of Daniel Soluk, University of Alberta). A *Metretopus* sp. population, probably *M. borealis*, also had a univoltine winter cycle in Swedish Lapland (Ulfstrand 1969).

Oligoneuriidae

Most members of this family exhibit summer cycles (Table 5). All *Oligoneuriella* species, mainly *O. rhenana*, have univoltine summer cycles. The two *Lachlania* species also have summer cycles. In contrast, the life cycle report for *Elassoneuria insulicola* indicates a seasonal univoltine winter cycle in a high altitude stream of Madagascar (Ramanankasina 1973).

Table 8. Tabular summaries: *Ephemera* and *Hexagenia*.

	Species			Life Cycles		
	No.	% Gen.	% All	No.	% Gen.	% All
<i>Ephemera</i>						
Total Univoltine	4	66.7	1.8	9	37.5	2.0
Uw	4	66.7	2.8	9	37.5	3.0
Total						
Semivoltine	4	66.7	33.1	13	54.2	46.4
2Y	4	66.7	33.1	11	45.8	42.3
3Y	1	16.7	100.0	1	4.2	100.0
2Y-3Y	1	16.7	100.0	1	4.2	100.0
Total Uni-						
Semivoltine	1	16.7	14.2	2	8.3	18.2
Uw-2Y	1	16.7	14.2	2	8.3	18.2
Totals	6			24		
<i>Hexagenia</i>						
Total Univoltine	2	50.0	0.9	6	26.1	1.3
Uw	2	50.0	1.4	6	26.1	2.0
Total						
Multivoltine	1	25.0	0.9	1	4.4	0.5
MB	1	25.0	1.6	1	4.4	0.7
MBws	1	25.0	2.0	1	4.4	0.9
Total						
Semivoltine	3	75.0	25.0	10	43.5	35.7
2Y	3	75.0	25.0	10	43.5	38.4
Total Uni-						
Semivoltine	3	75.0	42.9	6	26.1	54.5
Uw-2Y	3	75.0	42.9	6	26.1	54.5
Totals	4			23		

Table 9. Heptageniidae tabular summary.

	Species			Life Cycles		
	<i>No.</i>	<i>% Fam.</i>	<i>% All</i>	<i>No.</i>	<i>% Fam.</i>	<i>% All</i>
Total Univoltine	79	92.9	36.2	139	81.3	30.6
Uw	58	68.2	40.9	106	62.0	35.8
Us	19	22.4	23.8	28	16.4	19.9
Us-Uw	5	5.9	71.4	5	2.9	55.6
Total						
Multivoltine	19	22.4	17.4	27	15.8	12.4
M?	1	1.2	33.3	1	0.6	25.0
MB	12	14.1	18.8	18	10.5	12.5
MBss	1	1.2	5.3	1	0.6	3.9
MBws	11	12.9	22.5	17	9.9	14.9
MP	2	2.4	10.5	2	1.2	10.0
MNP	6	7.1	17.1	6	3.5	13.0
Total Uni-						
Multivoltine	1	1.2	14.3	1	0.6	14.3
Uw-MBws	1	1.2	25.0	1	0.6	25.0
Total						
Semivoltine	1	1.2	8.3	1	0.6	3.6
2Y	1	1.2	8.3	1	0.6	3.9
Total Uni-						
Semivoltine	3	3.5	42.9	3	1.8	27.3
Uw-2Y	3	3.5	42.9	3	1.8	27.3
Totals	85			171		

Table 10. Number of life cycles of each type reported for (1) *Rhithrogena semicolorata*, (2) *Ecdyonurus venosus*, (3) *E. torrentis*, (4) *E. lateralis* (= *Heptagenia lateralis*), (5) *Heptagenia sulphurea*, (6) *Stenonema tripunctatum*, and (7) *Stenacron interpunctatum*.

	1	2	3	4	5	6	7
Total Univoltine	13	4	4	6	3	3	2
Uw	13	4	4	6	3	3	2
Total							
Multivoltine	1	5	1	—	1	2	3
M?	—	—	1	—	—	—	—
MB	1	5	—	—	1	2	1
MBws	1	5	—	—	1	2	1
MP	—	—	—	—	—	—	1
MNP	—	—	—	—	—	—	1
Total Uni-							
Multivoltine	—	—	—	—	—	—	1
Uw-BMws	—	—	—	—	—	—	1
Total							
Semivoltine	—	—	—	—	—	—	1
2Y	—	—	—	—	—	—	1
Total Uni-							
Semivoltine	—	—	—	—	1	—	—
Uw-2Y	—	—	—	—	1	—	—
Totals	14	9	5	6	5	5	7

Table 11. Leptophlebiidae and Polymitarcidae tabular summaries.

	Species			Life Cycles		
	<i>No.</i>	<i>% Fam.</i>	<i>% All</i>	<i>No.</i>	<i>% Gen.</i>	<i>% All</i>
Leptophlebiidae						
Total Univoltine	21	63.3	9.6	59	78.7	13.0
U?	3	3.0	12.5	1	1.3	11.1
Uw	13	39.4	9.2	45	60.0	15.2
Us	10	30.0	12.5	13	17.3	9.2
Total						
Multivoltine	13	39.4	11.9	15	20.0	6.9
M?	1	3.0	33.3	1	1.3	25.0
MB	3	9.1	4.7	4	5.3	2.8
MB?	1	3.0	20.0	1	1.3	25.0
MBws	2	6.1	4.1	3	4.0	2.6
MP	1	3.0	5.3	1	1.3	5.0
MNP	7	21.2	20.2	9	12.0	19.6
Total Uni-						
Multivoltine	1	3.0	14.3	1	1.3	14.3
Uw-MBws	1	3.0	25.0	1	1.3	25.0
Totals				33	75	
Polymitarcidae						
Total Univoltine	3	60.0	1.4	7	50.0	1.5
Uw	3	60.0	2.1	3	21.4	1.0
Us	2	40.0	2.5	4	28.6	2.8
Total						
Multivoltine	1	20.0	0.9	6	42.0	2.8
MNP	1	20.0	2.9	6	42.9	13.0
Total						
Semivoltine	1	20.0	8.3	1	7.1	3.6
2Y	1	20.0	8.3	1	7.1	3.9
Totals				5	14	

Table 12. Number of life cycles of each type reported for (1) *Paraleptophlebia submarginata*, (2) *P. debilis*, (3) *Leptophlebia vespertina*, (4) *L. marginata*, (5) *Habrophlebia lauta*, and (6) *Habroleptoides modesta*.

	1	2	3	4	5	6
Total Univoltine	7	3	8	5	7	5
Uw	7	—	8	5	6	5
Us	—	1	—	—	1	—
Total						
Multivoltine	—	2	—	—	—	—
M?	—	1	—	—	—	—
MB	—	1	—	—	—	—
MBws	—	1	—	—	—	—
Totals	7	5	8	5	7	5

Table 13. Siphonuridae and Tricorythidae tabular summaries.

	Species			Life Cycles		
	<i>No.</i>	<i>% Fam.</i>	<i>% All</i>	<i>No.</i>	<i>% Fam.</i>	<i>% All</i>
Siphonuridae						
Total Univoltine	19	86.4	8.7	36	92.3	7.9
U?	2	9.1	25.0	2	5.1	22.2
Uw	10	45.5	7.0	20	51.3	6.8
Us	11	50.0	13.8	12	30.8	8.5
Us-Uw	1	4.5	14.3	2	5.1	22.2
Total						
Multivoltine	2	9.1	1.8	2	5.1	0.9
MB	1	4.5	1.6	1	2.6	0.7
MBws	1	4.5	2.0	1	2.6	0.9
MNP	1	4.5	2.9	1	2.6	2.2
Total Uni-						
Multivoltine	1	4.5	14.3	1	2.6	14.3
Us-MBss	1	4.5	33.3	1	2.6	33.3
Totals	22			39		
Tricorythidae						
Total Univoltine	3	50.0	1.4	3	30.0	0.7
Us	3	50.0	3.8	3	30.0	2.1
Total						
Multivoltine	5	83.3	4.6	7	70.0	3.2
MB	2	33.3	3.1	2	20.0	1.4
MBss	1	16.7	5.3	1	10.0	3.9
MBws	1	16.7	5.3	1	10.0	0.9
MP	1	16.7	2.9	2	20.0	10.0
MNP	3	50.0	8.6	3	30.0	6.5
Totals	6			10		

Table 14. Number of life cycles of each type reported for (1) *Ephemera danica*, (2) *E. simulans*, (3) *Hexagenia limbata*, (4) *H. bilineata*, (5) *Povilla adusta*, (6) *Siphonurus lacustris*, and (7) *Ameletus inopinatus*.

	1	2	3	4	5	6	7
Total Univoltine	3	4	3	3	—	6	9
Uw	3	4	3	3	—	2	9
Us	—	—	—	—	—	2	—
Us-Uw	—	—	—	—	—	2	—
Total							
Multivoltine	—	—	—	1	—	—	—
MB	—	—	—	1	—	—	—
MBws	—	—	—	1	—	—	—
MNP	—	—	—	—	6	—	—
Total							
Semivoltine	4	4	4	—	—	—	—
2Y	2	4	4	—	—	—	—
3Y	1	—	—	—	—	—	—
2Y-3Y	1	—	—	—	—	—	—
Total Uni-							
Semivoltine	2	—	4	1	—	—	—
Uw-2Y	2	—	4	1	—	—	—
Totals	9	8	11	5	6	6	9

Polymitarcidae

Polymitarcids exhibit several types of life cycles (Table 11). The two major *Ephoron* species, the Palearctic *E. virgo* and the Nearctic *E. album*, each exhibit both univoltine winter cycles and univoltine summer cycles. Scott *et al.* (1959) report *Tortopus incertus* populations in Georgia, USA, to have a two-year cycle, although recently Berner (see McCafferty 1975) suggests several broods in a year. Clearly more life cycle information is needed for this burrowing mayfly.

Relatively extensive data for the tropical *Povilla adusta* indicate a non-seasonal polyvoltine cycle (Table 14). In some areas of Africa, *P. adusta* adults exhibit a lunar cycle of emergence (Hartland-Rowe 1955), but in other areas they do not (Hartland-Rowe 1958, Petr 1970). Generation time has been estimated for several *P. adusta* populations and ranges from three to possibly six months (Corbet 1957, Corbet *et al.* 1974, and Bidwell 1979).

Potamanthidae

Life cycle data are available for two potamanthid genera. *Potamanthus* populations, both Palearctic and Nearctic species, have univoltine winter cycles; and one species, *P. myops*, usually requires two years to complete the cycle in Michigan, USA (Bartholomae and Meier 1977). One report for the tropical *Potamanthodes* indicates a non-seasonal cycle.

Siphonuridae

***Siphornurus* Eaton, *Ameletus* Eaton and *Isonychia* Eaton**

Members of this primitive and widely distributed family exhibit mainly univoltine cycles, with a relatively large number of univoltine summer cycles (Table 13). About half of all siphonurid species for which there were voltinism data have at least one summer cycle. *Siphornurus* populations are characterized as having summer cycles, usually univoltine but sometimes bivoltine. The lentic *S. lacustris* accounts for all univoltine winter cycles of *Siphornurus*, but some *S. lacustris* populations exhibit summer cycles (Table 14). Although not indicated in the tabular summary, Bretschko (1966) and Landa (1968, 1969) suggest some populations might occasionally have a bivoltine (MBws) cycle. *Ameletus* populations are also univoltine, but with relatively more winter cycles than summer cycles. The nine life cycle reports for the Palearctic *A. inopinatus* indicate an entirely univoltine winter species (Table 14). The few life cycle data for *Isonychia* populations give no indication of a characteristic cycle; however, when more information is available, perhaps summer cycles will be the characteristic type for temperate *Isonychia* species. Seasonal cycles for tropical *Isonychia* species are not indicated.

Other Siphonurid genera

The few life cycle data for other siphonurids indicate summer cycles for *Siphonisca*, *Parameletus* and *Aneletris* populations. Populations of the Australian *Oniscigaster wakefieldi*,

perhaps one of the most primitive of recent mayflies (Edmunds 1957b), have univoltine winter cycles (McLean 1970). *Coloburiscus humeralis*, another Australian species, is also a univoltine winter species (Wisely 1965).

Tricorythidae

Except for adult records indicating non-seasonal cycles (MNP) for *Tricorythus maculatus* and *T. tinctus* in Uganda (Tjønneland 1960), I could find complete life cycle data only for the Nearctic-Neotropical *Tricorythodes* (Table 13). Generally, temperate populations of *Tricorythodes* are characterized as multivoltine. Two species, *T. atratus* and *T. minutus*, have been studied in detail. *Tricorythodes atratus* apparently is a summer species, with one or more summer generations (e.g. Hall *et al.* 1975). In contrast, *T. minutus* populations appear more flexible in their voltinism. Newell and Minshall (1978) reported *T. minutus* populations to have several generations (MP) a year (with the adults on-the-wing during every month except February) in an Idaho, USA, stream having a constant 18°C water temperature. In contrast, in a typical stream (normal seasonal water temperature fluctuations) of the same area, the population was bivoltine (MBWs). Flight data of *Tricorythodes* sp. in Florida give no indication of a seasonal cycle.

Other Families

The other families are either monogeneric or voltinism data are available for only one genus. All members of the northern, Holarctic *Ametropus* (Ametropodidae) have univoltine winter cycles. Voltinism data, available for five species, account for six univoltine cycles; *A. neavei*, *A. albrighti*, and *A. ammophilus* are Nearctic; *A. eatoni* and *A. fragilis* are Palearctic. The three species of the Nearctic *Baetisca* (Baetiscidae) for which there were adequate voltinism data, *B. bajkovi*, *B. obesa* and *B. rogersi*, have univoltine winter cycles; the seasonal cycle is even maintained by *B. rogersi* populations in Florida (Pescador and Peters 1974).

Dolania americana (Behningiidae), a burrowing mayfly, has a two-year cycle in the southeastern USA, although most of the first year is spent in the egg stage (Harvey *et al.* 1980). Ramanankasina (1973) reported a *Probosciodoplocia sikorai* (Euthypolciidae) population to have a univoltine winter cycle in a high elevation (ca. 1450 m) river of Madagascar. *Neoephemeropsis* (Neoephemeridae) was apparently non-seasonal in Malaysia. *Palingenia* (Palingeniidae) has been stated to have a three-year cycle, but this is not based on a complete life cycle study. There is very little life cycle information available for *Prosopistoma* (Prosopistomatidae). Alouf (1977) presents a growth histogram for *P. oronti* of Lebanon and indicates the population probably has a univoltine cycle. There apparently are no voltinism data for the single siphlaenigmatid species.

Synopsis

Because few reports were available from the tropics, percentages for the total mayfly fauna (Table 1) do not reflect the true proportions of global mayfly life cycle types; they probably give a more accurate picture of Northern Hemisphere life cycle types. For the entire fauna, the univoltine cycle is commonest, with about three-fourth of all species for which voltinism data are available having at least one univoltine cycle (Table 1). The most reported single life cycle

type is the univoltine winter cycle. Multivoltine cycles, including the non-seasonal cycles, account for about a third of all cycles. The semivoltine cycles and the cycles judged variable (i.e. uni-multivoltine and uni-semivoltine) each account for less than 5% of the life cycles reported.

The small number of variable-type cycles reported does not indicate extent of flexibility in mayfly life cycles, because variable-type cycles include only cycles where voltinism of a given species for a particular study was variable, depending on year, local habitat, or from the same egg cohort. In addition, for many species (indeed, most species having several life cycle reports) different studies indicated different types of voltinism. Even allowing for some erroneous interpretations, there is much evidence for life cycle flexibility in many, although not all, mayfly species. Members of Baetidae mainly *Baetis* and *Cloeon*, and Ephemeridae, mainly *Hexagenia*, account for more than half of the variable life cycle reports. Within Baetidae, the variability is mainly bivoltine (MBws)--univoltine winter cycles; within Ephemeridae, semivoltine (2Y)--univoltine winter cycles.

Members of Baetidae, Leptophlebiidae, and Heptageniidae, account for most non-seasonal cycles. Mayflies with non-seasonal cycles are tropical or semi-tropical. A few mayflies from temperate regions, during certain years, were reported emerging every month of the year, especially a few species from the French Pyrenees, western Oregon, and England. But other life cycle features, especially nymphal growth, indicate seasonality for these mayflies. There were no indications of seasonal cycles for mayflies placed in the non-seasonal polyvoltine type; but many of these life cycles were based on yearly adult records, with few observations of other life stages.

Certainly, much is to be learned about tropical mayfly life cycles, *Povilla adusta* being the only tropical mayfly thoroughly studied. Generally, non-seasonality can be equated with multivoltinism, such as done in this report, but non-seasonality, as indicated by emergence throughout the year, would not seem to be invariably associated with multivoltine cycles. Thorough studies of all life cycle stages of tropical mayflies, especially nymphal growth, would be valuable and might reveal a surprisingly large number of seasonal cycles in the tropics.

SUMMER CYCLES

About a third of all mayfly species of this report exhibit at least one exclusively summer cycle (i.e. Us, MBss, Us-MBss). The summer cycle features a long winter period of egg dormancy, resulting in absence of the nymphal population from aquatic habitats for usually seven or more months of the year. Such variation in periodicity, when it occurs in large numbers of organisms, has important implications for design and interpretation of a variety of studies pertaining to whole community processes. For example, nymphal periodicity can be a very important parameter in estimating secondary production of aquatic invertebrates. It would therefore seem instructive to examine summer cycles of mayflies in more detail.

Species of Baetidae (mainly *Baetis* and Ephemerellidae (mainly *Ephemerella*) account for almost half of the exclusively summer life cycles, with *Ephemerella ignita* populations accounting for almost a third of these cycles. At least 50% of the species in Oligoneuriidae, Siphonuridae and Tricorythidae have at least one summer cycle.

The summer cycle in mayflies seems to be mainly facultative, because most of the thoroughly studied species exhibiting a preponderance of summer cycles, e.g. *B. scambus*, *E. ignita*, *P. debilis*, also occasionally have an overwintering nymphal population. It would be

instructive to know whether the summer cycle is obligate or facultative for *Oligoneuriella rhenana*, one species with several life cycle reports but none indicating an overwintering nymphal generation.

There is evidence (Bohle 1972, Elliott 1978, and Humpesch 1980) that water temperature is the primary factor in controlling hatching time of mayfly eggs and therefore determining whether a summer cycle will take place. The water temperature-hatching time relationship is not necessarily a simple one. For example, in warm lowland streams of Europe, *E. ignita* nymphs are sometimes found throughout the year (in contrast to the typical summer cycle in colder upland streams). Elliott's (1978) combined laboratory-field study showed that these higher water temperatures in lowland streams in autumn and winter shorten hatching time of *E. ignita* eggs; whereas in the same stream, temperatures above ca. 14.5°C in spring and summer lengthen hatching time. The overall effect of higher temperatures in lowland streams is therefore to extend hatching time over several months.

Adaptive significance of the summer cycle in insects generally is considered to revolve around the long egg stage, namely an adaptive response to uncertainties of harsh winter conditions, what might be considered an adaptation to high probability events. However, many mayfly populations exhibit summer cycles in aquatic environments where physical conditions appear no more stressful in winter than in summer. Of course, at high altitudes or latitudes, the possibility of stressful winter conditions, especially water freezing into the substrate, is more obvious. In such localities, a relatively large number of mayfly populations exhibit summer cycles (Clifford 1969, Andersen *et al.* 1978).

In localities where winter conditions do not appear especially stressful, adaptive significance of the summer cycle might relate more to the short nymphal stage in summer than to the long egg stage of winter. For example, a brief nymphal stage might minimize predation. Also, because nymphs of summer species are usually exposed to a relatively greater autochthonous food supply than are overwintering nymphs, one might suspect a correlation between herbivory and summer species, in contrast to detritivory and winter species. As discussed in the Reproductive Section, univoltine summer mayflies usually emerge and hence reproduce later in the year than do univoltine winter species. But the adaptive significance of this temporal isolation in the reproductive period of the two types seems obscure, since there would appear to be very little competitive interaction for these non-feeding, short-lived adults.

EGG DORMANCY IN SUMMER

The life cycle scheme used here does not distinguish what might be considered the opposite of the summer cycle, namely a cycle featuring a long egg stage (probably a true diapause) in summer instead of winter. Recently Masaki (1980) summarized much of what is known about summer diapause in temperate insects. The phenomenon is common and widespread, especially pupal and adult summer diapause for terrestrial insects of several holometabolous orders, but not so common for aquatic hemimetabolous insects; for example, Masaki gives only one citation (summer egg-stage diapause) for Ephemeroptera.

I arbitrarily considered summer egg-stage dormancy to exist in Northern Hemisphere mayflies with univoltine cycles if between April and October there were at least four months between emergence and appearance of the new generation. Only reports where there appeared to be routine sampling throughout the summer were considered. The four-month period would seem a conservative criterion, because three and even two months in the egg stage would

probably indicate dormancy in the sense of delayed hatching of some sort. However, it is sometimes difficult to find very small nymphs by the usual sampling methods, especially if a fine mesh net is not used, and one relatively long interval between the summer samples could lead to an erroneous interpretation of the new generation's appearance; it would therefore seem best to be conservative in this regard.

Based on the four-month criterion, the following mayflies qualify as exhibiting summer egg-stage dormancy. BAETIDAE: *Centroptilum elsa* (Lehmkuhl 1973a). EPHEMERELLIDAE: *Ephemerella dorothea* (Sweeney and Vannote 1978), *E. notata* (Landa 1968), *E. mucronata* (Landa 1968), *E. subvaria* (Sweeney and Vannote 1978). *Serratella deficiens* (Coleman and Hynes 1970), *Eurylophella versimilis* (Sweeney and Vannote 1978); CAENIDAE: *Caenis rivulorum* (Thibault 1971b). HEPTAGENIIDAE: *Rhithrogena morrisoni* (Lehmkuhl 1970), *R. hercynia* (Landa 1968), *R. germanica* (Landa 1968), *Heptagenia fuscogrisea* (Landa 1968), *Ecdyonurus quadrilineatus* (Landa 1968). LEPTOPHLEBIIDAE: *Leptophlebia marginata* (Landa 1968). SIPHLONURIDAE: *Siphonurus occidentalis* (Lehmkuhl 1973a).

These 15 life cycles make up only a small fraction of the total 296 univoltine winter cycles reported. However, when these summer dormancy cycles are considered as a proportion of total winter cycles where the presence or absence of egg-stage dormancy could be deduced (175), then the 15 cycles represent about 10% of the univoltine winter cycles; and the percentage would be 16% if the criterion for summer dormancy was three months instead of four. Probably even this is an underestimate of summer egg-stage dormancy, a phenomenon not very amenable to field analysis. Also, there are instances where part of the population's egg cohort undergoes what would qualify as summer egg-stage dormancy; for example, the eggs of *Leptophlebia cupida* in a brown-water stream of Alberta, Canada, start hatching in July, but continue to hatch for four or five months after emergence of the old generation is completed; this has been verified both in the field (Clifford 1969) and in the laboratory (Clifford *et al.* 1979).

The obvious adaptive value of summer egg-stage dormancy, be it a facultative or obligatory phenomenon (Pleskot 1962 suggests it is facultative), would seem to involve tiding the population over unfavorable summer conditions. The 15 life cycles were reported from only 5 localities; but of these, in only one, western Oregon (Lehmkuhl 1969), were harsh physical conditions in summer, namely high summer temperatures and very low flow, reported. Regardless of adaptive value of summer egg-stage dormancy in mayflies (and, as for winter egg-stage dormancy, one could suggest several possibilities), the phenomenon appears common enough in mayflies to merit much more study. Any phenomenon that removes the obvious aquatic stage from streams or lakes for long periods has important implications in the analysis of aquatic communities.

LIFE CYCLE TYPES AND PRODUCTION

The Hynes method (Hynes and Coleman 1968), or size-frequency method, in which the secondary production estimate is based on average cohorts instead of true cohorts, is one of the most widely used methods to estimate production of aquatic invertebrates, especially insects. The method was originally used to estimate yearly production of the entire benthic fauna, but it appears to be most accurate when applied to single species or groups of species with similar life cycle features (Benke 1979, Waters 1979).

The yearly production estimate by the Hynes method does not account for populations with more than or less than one generation a year. To correct for this, the usual procedure, first proposed by Hamilton (1969), is to multiply the yearly Hynes estimate by the number of generations per year of the population in question, e.g. two for bivoltine populations and 0.5 for two-year semivoltine populations. Benke (1979) pointed out if the population spends a considerable part of the year in a non-larval stage an error in the production estimate might result by using these correction factors for bivoltine and semivoltine populations or by using no correction factor for all types of univoltine populations. He proposed a correction factor based on cohort production interval (CPI). This is essentially the yearly nymphal periodicity of the population in days (or months).

I recorded nymphal periodicity (in months) for species of all life cycle types and therefore could consider how these correction factors might influence production estimates of mayflies exhibiting various life cycle types. The usual procedure is to apply no correction value to the Hynes estimate when calculating production of organisms with univoltine cycles; and this would seem valid for most univoltine winter mayflies, because the average correction factor of the 175 univoltine winter cycles was very close to 1, namely 1.09 (\bar{x} CPI = 11.0 months, S.E.=0.14, R=7-15 months). Exceptions are the univoltine winter mayflies with a lengthy egg-stage dormancy in summer (see preceding section). For these 15 univoltine winter cycles, the average correction factor would be 1.54 (\bar{x} CPI = 7.8 months, S.E.=0.14, R=7-8 months), and if not applied to the Hynes estimate would result in yearly production of these univoltine winter populations being underestimated.

Not applying a correction factor to univoltine summer mayflies, assuming production estimate is based on data collected throughout the year, would result in serious errors of production estimates. The mean CPI of the 102 univoltine summer cycles was 4.1 months (S.E.=0.13, R=2-7 months); the resulting correction factor is 2.92 and if not applied to the Hynes estimate would result in large underestimates of production. But, these culled, average values should be considered a tenuous substitute for empirically derived values, because the range of CPI values for summer mayflies was two to seven months (with a tendency for shorter CPI's at higher latitudes and altitudes).

A feature of most univoltine summer cycles of mayflies is that nymphal growth is often easy to interpret accurately, because hatching is synchronous and the nymphal stage is quite brief. If sampling intervals are short, the population can usually be followed as a single cohort, and the Hynes estimate without the correction factor or one of the definitive cohort-based methods (Waters 1979 discusses these) would appear sufficient for a realistic estimate of production.

For the 69 bivoltine winter-summer cycles, average CPI was 9.5 months (S.E.=0.21, R=7-12 months) for the winter generation and 4.1 (S.E.=0.17, R=2-9 months) for the summer generation; the average CPI for the two generations would be 6.8. But this value is not valid for calculating a yearly correction factor for bivoltine populations, because the average CPI of both generations can not be more than six months, i.e. the average individual of one generation must reach adulthood, mate, and lay eggs before the average individual of the next generation begins larval development (Benke, A.D., Georgia Institute of Technology, personal communication). Benke (pers. comm.) suggests the most accurate way to treat multivoltine populations is to apply the Hynes estimate to each generation separately and then add the separate values together to obtain annual production (see Menzie C.A. 1980. A note on the Hynes method of estimating secondary production. *Limnology and Oceanography* 25:770-773).

A modification pertinent for bivoltine winter-summer mayflies might be to calculate a "weighed" average for the two generations, because individuals of the summer generation usually are much smaller than those of the winter generation for a given developmental age, perhaps by as much as 20%.

For the 10 semivoltine cycles (disregarding the three-year cycles) where total life span was reported in months instead of years, the mean CPI was 23.8 (S.E.=0.51) and the resulting correction factor of 0.504 would of course indicate that the usual correction factor of 0.5 would be valid for most two-year semivoltine mayflies. But even here, there is no substitute for empirically derived values, as the CPI's ranged from 21 to 27 months.

The average CPI's and resulting correction factors are for life cycle types, not for species, and they will usually vary much less for life cycle type than for individual species. There would appear to be a much greater danger in using the average CPI values of this report for individual species, especially wide-ranging species, than for life cycle types, because of the life cycle flexibility exhibited by many species. To use an extreme example, the CPI of *Hexagenia bilineata* ranged from 4.3 to 24.0 months.

LIFE CYCLE TYPES AND REPRODUCTION

Because the adult stages of mayflies are short, seldom more than three days, adult records can generally be equated with reproduction period. Adult periodicity for mayflies is usually derived from emergence data. However, it would seem possible, especially for mayflies with long emergence periods, to have synchrony within the period, resulting in an "effective" adult period, accounting for most of the successful reproduction, and a total adult period, which might be longer than the reproductive period. I know of no studies that have investigated this, and for purposes here, the premise is that the total adult period is equated with the total reproductive period.

I recorded for all Northern Hemisphere mayflies having seasonal cycles the months of emergence (or other adult periodicity data) for species of each life cycle type. Numerous other studies report complete emergence data but not species' voltinism (see Methods); these were treated separately. Reproductive periods for the entire Northern Hemisphere fauna and for each of the major life cycle types are shown in Figure 2. Reproductive periods of important species, each representing one of the life cycle types, are shown in Figure 3. With the exception of *Leptophlebia vespertina*, each of these species was occasionally reported as having other major life cycle types as well (see General Analysis), but only adult data associated with the species' life cycle type in question were used in compiling the line graphs.

Each major voltinism type appears to have a characteristic seasonal reproductive period (Fig. 2A, B). The line graph indicating the total reproductive period of all Northern Hemisphere mayflies very much resembles a yearly water temperature curve for north-temperate regions (Fig. 2C). Almost half of mayfly reproduction in the Northern Hemisphere takes place during June and July; obviously when considered on a hemisphere basis, the word mayfly is a misnomer. The multivoltine mayflies have the most extensive reproductive period (Fig. 2A). (The commonest multivoltine cycle is the bivoltine winter-summer cycle, and the two minor peaks probably reflect the maximum reproductive period for each of these generations). The semivoltine mayflies appear to have the most restrictive total reproductive period (Fig. 2A). Populations of univoltine summer mayflies generally reproduce later than do the univoltine winter mayflies (Fig. 2B). The total reproductive periods of individual species, each exhibiting a major life cycle type, were quite similar to those of the life cycle types (Fig. 3).

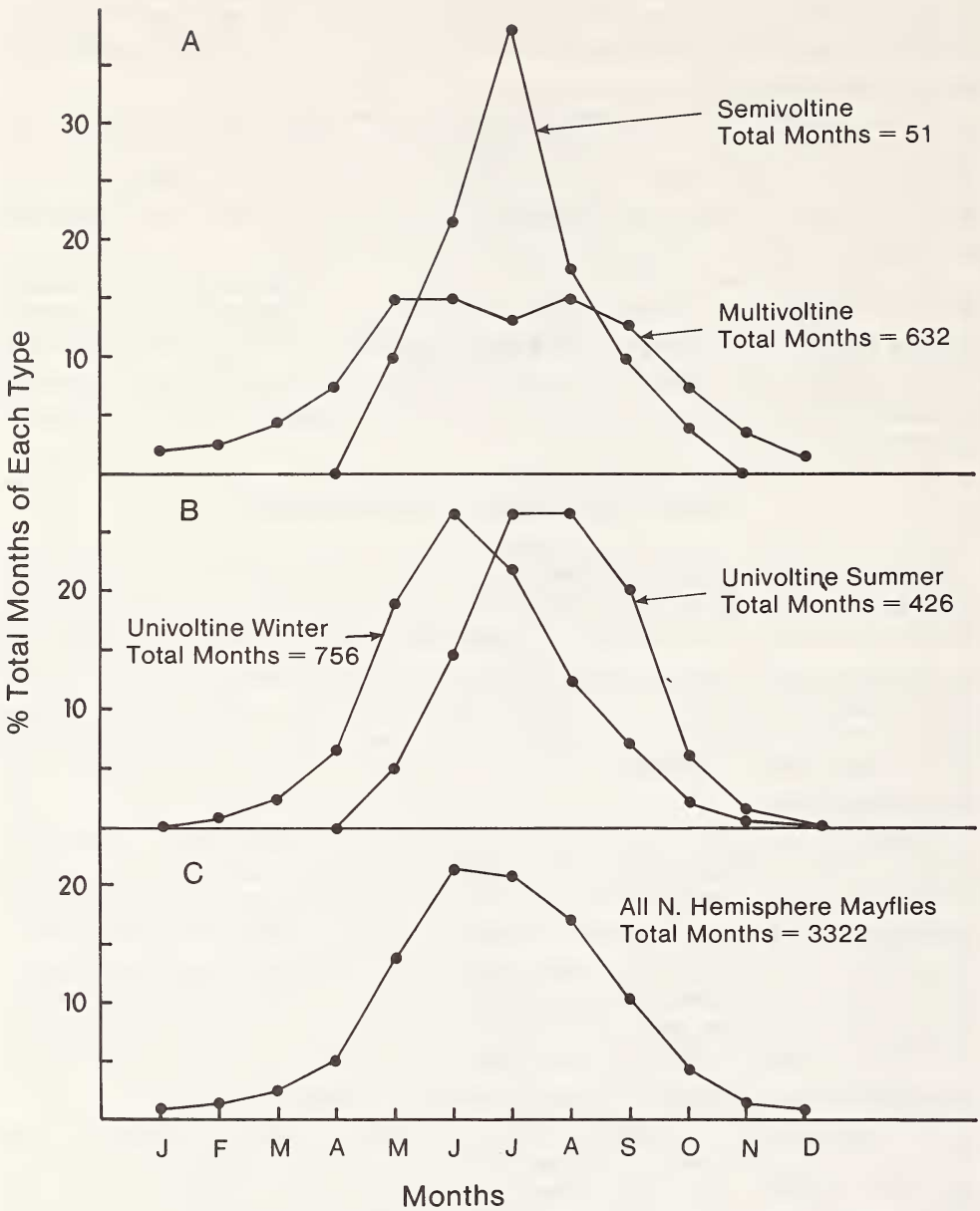


Figure 2. Percentage monthly reproductive period (equated with adult periodicity) for Northern Hemisphere mayflies of each life cycle type (based on complete voltinism data) and all Northern Hemisphere mayflies, regardless of life cycle type (based on complete voltinism data and also data of studies pertaining exclusively to adult periodicity). Total months are the total number of months that all species of a particular life cycle type were reported as adults; e.g. in January, there were 14 reports ($14/632 = 2.2\%$) of multivoltine species being reported in the adult stage.

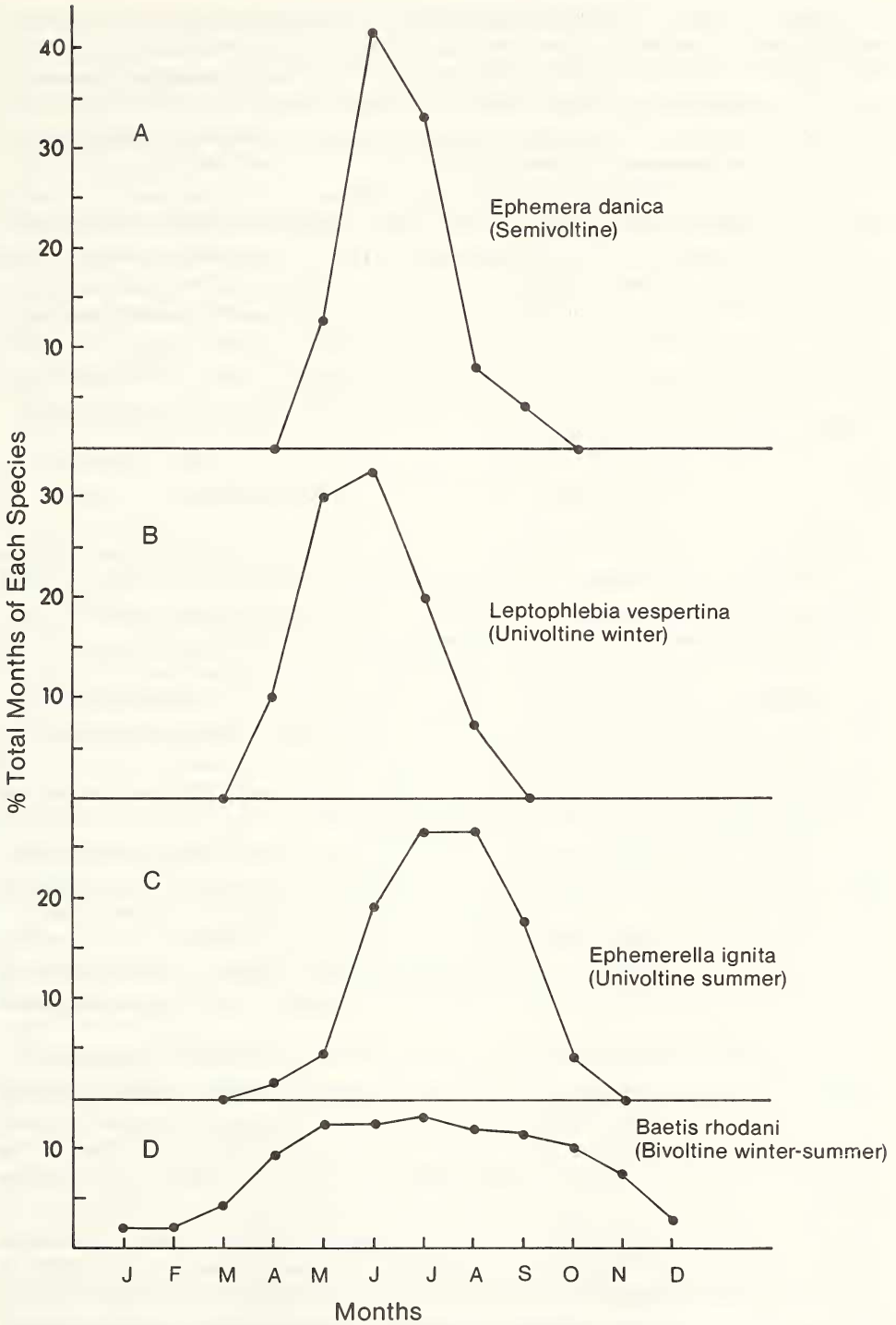


Figure 3. Percentage monthly reproductive period for four species (throughout their range), each representing one life cycle type.

Using words similar to those used by Shapiro (1975) in discussing voltinism of butterflies, it would appear the semivoltine cycles of mayflies are associated with reproductive periods being shut down for the adverse season considerably before the average phenological properties of Northern Hemisphere environments would dictate they would have to be. In contrast, the reproductive period of multivoltine mayflies suggests reproduction continuing until deteriorating environmental conditions intervene.

It seems unusual that mayflies with the longest generation time, the semivoltine species, should have, when considered for all Northern Hemisphere localities, the shortest reproductive period, while mayflies with the shortest generation time, the multivoltine species, have the longest reproductive period. The adaptive strategy of the semivoltine cycle might be to minimize predation on adults, whereas the multivoltine cycle would minimize predation on nymphs. Edmunds and Edmunds (1980) discuss how adult periodicity patterns of mayflies might have been influenced by selective pressures of predators. Mackey (1978) discusses this specifically for *Caenis* species, one, *C. robusta*, having a long emergence period and another, *C. macrura*, having a short emergence period.

LIFE CYCLE TYPES AND OTHER FACTORS

There were no detectable trends between life cycle types and the various suggested phylogenetic schemes of extant myflies (e.g. Demoulin 1958, Edmunds 1972). No clear relationship between life cycle type and body size of individual species was noted. Many very small mayflies species, e.g. some baetids, caenids, tricorythodids, are multivoltine, and almost all the semivoltine species are relatively large mayflies, e.g. ephemerids; but numerous other large mayflies are not semivoltine. For mayflies of intermediate size no relationship between body size and life cycle type was evident. Total life spans (from hatching of eggs until death of the adult) vary from 3 years for *Ephemera danica* (Svensson 1977) to about 30 days, reported for the non-seasonal *Callibaetis floridanus* (Trost and Berner 1963) and the seasonal *Centroptilum pennulatum* (Macan 1978). Assuming a minimum egg incubation of 15-30 days for mayflies with very short life spans, in theory, at least, it would seem possible to have a maximum of six or more generations per year. No study, even for non-seasonal populations, has clearly demonstrated more than six generations a year, which appears to be maximum for a population of the non-seasonal *Povilla adustata*, although its populations usually had only four generations a year (Corbet *et al.* 1974). There have been suggestions of as many as six generations for seasonal mayflies; but for these, cohorts could not definitely be distinguished from generations.

For each life cycle study, latitude of the area in question was recorded, the hope being these latitudinal values when compared to life cycle types of that area would be amenable to analysis. However, variations in local conditions, e.g. continental vs. marine climates, altitudinal influences, etc., made such an analysis too difficult to interpret on a global basis. Nevertheless, mayfly life cycles ought to change in a predictable way going from tropics to arctic (Clifford *et al.* 1973).

In the tropics, mayflies exhibit mainly non-seasonal multivoltine cycles. In moderate temperate regions, the univoltine winter cycle is most common; however, all major life cycle types can be locally important. The univoltine winter cycle was the most reported of any life cycle type and probably in part reflects most life cycle studies in moderate temperate regions. In cold temperate and subarctic regions (disregarding areas influenced by marine climates)

there are fewer multivoltine cycles, relatively more semivoltine cycles, and a tendency for univoltine winter cycles to give way to the univoltine summer cycle. In the low and high arctic of continental climates, where mayflies species are few, the univoltine summer cycle predominates. Several terrestrial insects and even a few aquatic insects can have extraordinarily long semivoltine cycles in the arctic, while the same species are univoltine at lower latitudes. Semivoltinism is not a feature of arctic mayflies (the major semivoltine group, the ephemerids, are not found in the high arctic). Possibly, however, future studies, especially of the egg stage, may reveal semivoltine cycles for some of the arctic baetids and heptageniids, which, based on nymphal growth, have usually been reported as univoltine summer mayflies. For example, Ulfstrand (1968) reported *Heptagenia sulphurea* to be partly semivoltine at 65°, with one year probably spent in the egg stage.

DISCUSSION

The survey clearly indicates extensive life cycle flexibility for many mayflies. Admittedly, most species were reported as having only one life cycle type, but there were usually only one or two complete life cycle studies for most species. The more thoroughly a species is studied throughout its range, the more flexible its life cycle usually appears. In fact, the variability that most species show in their life cycle types appears to be directly correlated with the number of studies reported for that species. Several workers, e.g. Ulfstrand (1968), Lehmkuhl (1973a), Flowers and Hilsenhoff (1978), Whelan (1980), have commented on plasticity of mayfly life cycles for certain species, but most workers probably feel there is an inherent rigidity in the life cycle of most species--at least to where the type voltinism does not change.

The bet-hedging and risk-spreading strategies of a flexible life cycle seem so obvious (e.g. partitioning of different foods among different sizes of nymphs, advantages of several life stages being present if catastrophic events occur, etc.) that one might question how temperate mayflies with seemingly rigid life cycles manage not only to survive, given the uncertainties of the environment, but to be very abundant in certain areas. Populations of *Ameletus inopinatus* and temperate *Leptophlebia* are examples of this. In Alberta, *Leptophlebia cupida* is a very abundant mayfly; the species apparently always has a univoltine winter cycle, from year to year and from place to place. Life cycle data for *L. cupida* from other areas of North America also indicate a rigid univoltine winter cycle. And there are numerous life cycle reports for the Palearctic *L. vespertina* and *L. marginata*, all indicating a univoltine winter cycle. Clearly, the life cycle strategies of these successful *Leptophlebia* taxa must involve something other than flexibility in voltinism.

It is important to distinguish cohorts from generations. In many populations, the generation is essentially a single cohort; but in other populations there can be several groups of nymphs, each about the same age, growing at the same rate and transforming at the same time. Not accounting for cohorts can result in erroneous interpretations of life cycles; e.g. an apparent polyvoltine species where in fact there is a single generation of several cohorts. Where there were not sufficient data to distinguish cohorts from generations, some of the life cycles reported as univoltine winter cycle with a long emergence period could just as well have been interpreted as bivoltine winter-summer cycles; alternately, some of the bivoltine winter-summer cycles could have been interpreted as univoltine winter cycles, with the eggs hatching in pulses and resulting in cohorts. One criterion often used to distinguish the two generations of the bivoltine cycle is that the adults of the summer generation are often much smaller than the winter

generation adults. However, adults of univoltine mayflies transforming during the latter part of a long emergence season can also be much smaller than adults emerging early.

It is not always clear what is meant by a cohort. There are different gradations of cohorts. Ideally, nymphs of the same cohort will all transform at about the same time. Cohorts of this type might be so separated in time that it is questionable whether genetic mixing between cohorts of the same generation takes place. Sometimes there is a semblance of nymphal cohorts within the population, but the nymphs of each cohort tend to accumulate in a single potential-emerging-stage and then emerge as a single cohort (Clifford 1970a). In other species, the distinction between cohorts and generations is completely blurred; the population's eggs hatch at different rates, nymphs grow at different rates, and adults emerge and hence reproduce throughout the summer. An arbitrarily designated cohort in this type population might, at least in theory, contain nymphs of *different* generations. In short, the concept of distinguishing cohorts from generations is an important one; but, for mayflies (a group of insects that usually has a large and sometimes variable number of molts, which will further compound cohort analysis) in practice it would often seem very difficult, certainly without supplementary laboratory observations. Pritchard (1978) recently proposed a cohort-splitting hypothesis for the holometabolous crane-fly *Tipula*. Future modifications of this hypothesis may result in valuable information useful in analysing cohorts of mayflies.

FURTHER RESEARCH

Little life cycle information is available for several taxa frequently reported as locally abundant in standing crop studies, occasionally used as experimental animals, or occupying an interesting phylogenetic position. For the Northern Hemisphere fauna, these include: *Callibaetis* and *Heterocloeon* (Baetidae); *Dannella* (Ephemerellidae); *Pentagenia* and *Lithobrancha* (Ephemeridae); *Cinygma*, *Anepeorus*, *Pseudiron*, and *Spinadis* (Heptageniidae); *Traverella* and *Habroleptoides* (Leptophlebiidae); *Metretopus* (Metretopodidae); *Neoephemera* (Neoephemeridae); *Homooneuria* (Oligoneuriidae); *Palingenia* (Palingeniidae); *Tortopus* and *Campsuarus* (Polymitarcidae); *Prosopistoma* (Prosopistomatidae); *Isonychia* (Siphonuridae) and *Leptohyphes* (Tricorythidae). Much more life cycle information is also needed for all taxa of tropical mayflies, basing type voltinism on egg stage and nymphal growth data, as well as on adult periodicity.

A small number of genera in a few families usually account for most of the reports pertaining to number of animals per unit area of substrate (numerical abundance studies). For example, for the Holarctic region, species of *Baetis*, *Ephemerella*, *Rhithrogena*, *Hexagenia*, *Stenonema-Stenacron*, *Caenis* and *Paraleptophlebia* made up about 80% of the numerical abundance values reported in the literature (Clifford 1980). Concentrating life cycle studies on the abundant species of these genera might be a more feasible objective, in the sense of obtaining data about important mayfly contributors to the community, than attempting to work out the life cycle of every mayfly species in the community. In North America, *Hexagenia* populations are often an important biomass component of the community. Although there are considerable life cycle data for *Hexagenia* (though sometimes only reported at the generic level), more information on how the life cycle of the important *Hexagenia* species vary from region to region and year to year would be valuable.

Studies on how the various mayfly life cycle types relate to different methods of estimating secondary production would seem especially pertinent. Related to this is ability to distinguish

cohorts from generations. This is often not easy, but perhaps new methods will be developed to solve this problem (see, for example, the model relating egg hatching time to temperature presented by Elliott and Humpesch 1980).

The mayfly's egg stage is the least understood of the major life stages. Hatching time and other egg stage phenomena, e.g. predation on eggs (especially in cycles featuring a long egg stage), are not easy to study in the field. But a thorough understanding of the egg stage specifically and the role water temperature plays generally in influencing all life stages are the keys to better interpreting mayfly life cycles.

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APPENDIX--Species literature citations (by number) and consensus life cycles.¹

Ametropodidae

- Ametropus albrighti* Traver 8 Uw
A. amnophilus Allen and Edmunds 8 Uw
A. eatoni Brodskij 177 Uw
A. fragilis Albarda 196 Uw
A. neavei McDunnough 66,208 Uw

Baetidae

- Baetiella* sp. 277 MBws
B. japonica Imanishi 124 MB?
Baetis sp. 51,166,277,306,371 MBws
B. alpinus (Pictet) 158,160,161,180,196,321,323,330,341 see text
B. amplus (Traver) 51,250
B. atrebatinus Eaton 143,196 MBws
B. australis Traver 27
B. beskidensis Sowa 321 MBss
B. bicaudatus Dodds 191, 279 MBws
B. brunneicolor McDunnough 24,217 Us-MBss
B. buceratus Eaton 196,199,200,321 MBws
B. ephippiatus Traver 27

¹ Italicized citations indicate some voltinism data available; others refer to strictly adult periodicity, see Methods.

- B. flavistriga* McDunnough 24,217,226,250,289,327 MBss
B. frondalis McDunnough 24 MBss
B. fuscatus (L.) (= *B. bioculatus*) 116,117,143,196,199,200,
 261,295,296,321,323,354,355,368 MBss
B. gemellus Eaton 117,261,340 MP
B. gracilis Bogoescu and Tabacaru 321 Us
B. hageni Eaton 24,69,216 MBws
B. intercalaris McDunnough 24,27,217 Us
B. jesmondensis McDunnough 191
B. lapponicus (Bengtsson) 10,354,355 Us
B. lutheri Müller-Liebenau 161,321,323 no consensus
B. macani macani Kimmins 10,41,42,43,44,45,355 Us
B. macani bundyae Lehmkuhl 210 Us
B. macdunnoughi Ide 24,69,250 MBws
B. melanonyx (Pictet) 261,321 Us
B. meridionalis Ikonomov 261
B. muticus (L.) (= *B. pumilus*) 10,103,116,117,121,143,196,199,200,228,231,310,321,
 323,330,339,340,354,355,368 MBws
B. niger (L.) 10,99,128,143,153,196,314,321,,346 MBws
B. ochris Burks 289
B. persecuta McDunnough 137,191 MBws
B. propinquus (Walsh) 24,17,57,217,284 MBss
B. pygmaeus (Hagen) 24,27,217,270,284,289 MBws
B. rhodani (Pictet) 10,18,20,35,37,43,44,99,102,103,116,121,138,139,143,153,161,
 164,173,174,196,199,200,202,228,231,252,273,295,296,310,
 314,317,320,321,323,330,340,344,345,346,354, 355 see text
B. scambus Eaton 11,99,103,121,143,164,196,321,323,340,368 see text
B. sinaicus (Bogoescu) 321,323 MBss
B. soror Ulmer 331 MBws
B. subalpinus Bengtsson 278,295,296,354,355 no consensus
B. tricaudatus Dodds (= *B. vagans*) 24,32,60,69,73,75,169,209,216,217,249,262,359,360
 see text
B. vardarensis Ikonomov 321,323 MBws
B. vernus (Curtis) (= *B. tenax*) 10,116,121,143,153,164,174,175,184,196,199,261,
 295,296,310,323,346 see text
B. yamatoensis Gose 125
Baetodes sp. 93 MNP
Callibaetis sp. 154,269
C. coloradensis Banks 32,60,137 M?
C. ferrugineus (Walsh) 140,217
C. floridanus Banks 27,81,351 MNP
C. praetiosus Banks 27,115 MNP
Centroptilum sp. 32,51,60,137,167 Us
C. album McDunnough 217
C. bellum McDunnough 51
C. corbeti Kimmins 347 MNP

- C. convexum* Ide 217
C. elsa Traver 209 Uw
C. fragile McDunnough 226
C. luteolum (Müller) 28,35,41,116,117,128,143,176,184,196,203,232,234,260,278,310,
 311,314,321,323,346,355,368 MBws
C. notabile Kimmins 347 MNP
C. pennulatum (Eaton) 143,196,232,260,311,321 no consensus
C. pulchrum Eaton 321 MBss
C. quaesitum McDunnough 51
C. rivulare Traver 51
C. rufustrigatum McDunnough 217,250,289,336 Us
C. simile McDunnough 299
C. viridocularis Berner 27 MNP
C. walshi McDunnough 25 MBss
Cloeon sp. 217
C. dentatum Kimmins 347 MNP
C. dipterum (L.) 35,41,47,52,53,78,95,126,143,153,176,184,187,196,200,223,231,258,
 313,321,346 see text
C. rubropictum McDunnough 27,40,51,226,289 MNP
C. samaeleni Gillies 40
C. simile Eaton 35,41,128,143,153,196,231,258,321,346,355 see text
C. simplex McDunnough 140
C. triangulifer McDunnough 118,327 MP
Dactylobaetis sp. 93
Heterocloeon sp. 93
Paracloeodes sp. 93
Procloeon bifidum (Bengtsson) 128,176,196,232,321,322 see text
P. ornatum Tshernova 321,322 MBss
Pseudocloeon sp. 51,137,140
P.alachua Berner 27 MNP
P. anoka Daggy 217
P. bimaculatum Berner 27 MNP
P. carolina Banks 250
P. dubium (Walsh) 57,226
P. inexpectatum Tshernova 321 MBss
P. myrsum Burks 271
P. parvulum McDunnough 27 MNP
P. punctiventris McDunnough 27,271 MNP

Baetiscidae

- Baetisca bajkovi* Neave 208 Uw
B. becki Schneider and Berner 283
B. laurentina McDunnough 217
B. obesa (Say) 57,207,217,226,284 Uw
B. rogersi Berner 28,284 Uw

Behningiidae

- Behningia ulmeri* Lestage 182
Dolania americana Edmunds and Traver 149,288 2Y

Caenidae

- Brachycercus* sp. 16 Us
B. flavenus Traver 140
B. harisellus Curtis 78,178,193,196,321 Us
B. lacustris (Needham) 217,226 Us
B. maculatus Berner 27,284 MNP
B. minutus Tshernova 196,321 U?
B. pallidus Tshernova 196,321 U?
B. prudens (McDunnough) 208 Us
Caenis sp. 31,166
C. amica Hagen 51
C. beskidensis Sowa 321,323 Us
C. delicata Traver 238
C. dimulata Walker 27,57,115,284 MNP
C. forcipata McDunnough 106,217,365 Uw
C. hilaris (Say) 27,284 MNP
C. horaria (L.) 41,128,143,153,176,178,196,236,253,258, 278,314,346 see text
C. jocosa McDunnough 217
C. latea Burmeister 196 Us
C. luctuosa Burmeister (= *C. moesta*) 22,41,143,196,260, 278,309 no consensus
C. macrura Stephens 116,143,178,196,200,236,321,340 MBws
C. noturna Bengtsson 278
C. pseudorivulorum Keffermuller 196,321 Us-MBss
C. rivulorum Eaton 11,103,178,184,237,273,321,340 Uw
C. robusta Eaton 34,178,196,236 no consensus
C. simulans McDunnough 32,132,137,140,217,226,289,306,336 no consensus
Tasmanocoenis tillyardi (Lestage) 331 MBws

Ephemerellidae

- Attenella margarita* (Needham) 4
Danella simplex (McDunnough) 5,217,246,284,329
Drunella coloradensis (Dodds) 6,98,122,301,371 Uw
D. cornuta (Morgan) 217,254
D. doddsi (Needham) 6,122,191,301,371 Uw
D. flavilinea (McDunnough) 6,137,148 Us
D. grandis grandis (Eaton) 6
D. grandis ingens (McDunnough) 6,371 Uw
D. lata (Morgan) 217
D. spinifera (Needham) 6,16,137 Uw
D. walkeri (Eaton) 217
Ephemerella aurivillii Bengtsson 14,202,218,220,321,354,355 Uw
E. basalis Imanishi 14,125,218,277,337 Uw

- E. catawba* Traver 51
E. choctawhatchee Berner 284
E. dentata Bajkova 218 Uw
E. dorothea Needham 51,217,336,357 Uw
E. excrucians Walsh 69,217 Uw
E. gracilis Tshernova 218
E. ignita (Poda) 11,12,13,14,17,46,50,78,82,84,95,96,99,100,102,103,116,117,
 121,129,143,164,173,178,185,196,199,200,201,203,218,220,227,
 228,231,233,237,239,260,272,273,282,290,295,296,310,312,314,
 321,323,330,339,340,364,368 see text
E. inermis Eaton 7,16,122,137,148,371 Uw
E. infrequens McDunnough 7
E. invaria (Walker) 140,217
E. kozhovi Bajkova 14,218 Us
E. lacustris Allen and Edmunds 7
E. latipes Tshernova 218 Uw
E. lenoki Tshernova 218
E. lepnenae Tshernova 218 Uw
E. levanidovae Tshernova 218 Uw
E. longicaudata Tshernova 125
E. mesoleuca (Brauer) 196,321 Us
E. mucronata Bengtsson (= *E. krieghoffi*) 196,218,220,310,321,354,355 Uw
E. needhami McDunnough 217
E. nigra Ueno 125,352 U?
E. notata Eaton 116,143,196,321,368 Uw
E. rufa Imanishi 125 MBws
E. rotunda Morgan 217
E. setigera Bajkova 218
E. subvaria McDunnough 54,217,265,336,362 Uw
E. tshernovae Bajkova 218
E. triacantha Tshernova 218,321 Us
E. trispina Ueno 125,277,337,352 Uw
E. yoshinoensis Gose 125,277,352 Us
E. zapekinae Bajkova 14,218
Eurylophella sp. 51
E. bicolor (Clemens) 57,226 Uw
E. funeralis (McDunnough) 104,136,336 Uw
E. lutulenta (Clemens) 57,217,226 Uw
E. minimella (McDunnough) 69
E. prudentialis (McDunnough) 51
E. temporalis (McDunnough) 106,140,217,226 Uw
E. trilineata (Berner) 27,284
E. versimilis (McDunnough) 336 Uw
Serratella deficiens (Morgan) 69,217,336 Uw
S. frisoni (McDunnough) 271
S. serrata (Morgan) 254,336 Us

- S. sordida* (McDunnough) 289
S. tibialis (McDunnough) 137,191,371 Uw
Teloganodes sp. 31 MNP
Timpanoga hecuba pacifica (Allen and Edmunds) 3
Torleya major (Klapalek) (= *T. belgica*) 129,196,260,296,321,323,339,340 Uw

Ephemeriidae

- Ephemer* sp. 31
E. amurensis Navas 218 Uw
E. blanda Traver 51
E. danica Müller 117,143,173,176,178,196,231,280,281,295,296,310,321,323,332,
 333,339,340,363 see text
E. formosana Ulmer 218
E. guttulata Pictet 183,243,299
E. japonica McLachlan 352 Uw
E. lineata Eaton 181,188,196,321 2Y
E. sachalinensis Matsumura 218
E. simulans Walker 27,38,49,57,69,106,114,137,140,168,208,217,226,243,249,
 263,289,304,324 see text
E. strigata Eaton 218
E. varia Eaton 299
E. vulgata L. 143,153,178,187,188,196, 260,278,314,321,346 2Y
Hexagenia sp. 51,77,111,225
H. atrocaudata McDunnough 217
H. bilineata (Say) 27,57,108,109,110,112,157,224,243,287,304,343 Uw
H. limbata Serville (+ *H. limbata limbata*) 32,76,77,93,105,106,109,140,155,156,
 157,163,217,226,243,264,265,289,308,
 325,334,372 see text
H. limbata oculata Walker 51,140,264,304,325 2Y
H. limbata viridescens (Walker) 140
H. munda Eaton 27,243
H. munda affiliata McDunnough 140
H. munda elegans Traver 27,51
H. munda marilandica Traver 27,51
H. munda orlando Traver 27
H. rigida McDunnough 105,140,217,243,264 2Y
Litobrancha recurvata (Morgan) 93,217,242,243,255,256,257,266,326
Pentagenia vittigera (Walsh) 109,113,243,289

Euthyplociidae

- Campylocia* sp. 93
Euthyplocia hecuba (Hagen) 93
Probosciplocia sikorai Vayssière 302 Uw

Heptageniidae

- Afronurus ugandanus* Kimmins 347 MNP

- Anepeorus* sp. 28
A. rusticus McDunnough 208 Us
Arthroplea bipunctata McDunnough 93,107,140 Us
A. congener Bengtsson 153,196,355 Us
Cinygma sp. 277 Uw
C. integrum Eaton 191,213 Uw
Cinygmula altaica Tshernova 218 Uw
C. grandifolia Tshernova 218 Uw
C. hirasana Imanishi 218
C. malaisei Ulmer 219 Uw
C. mimus (Eaton) 98,137 Uw
C. ramaleyi (Dodds) 148,301 Uw
C. reticulata McDunnough 191,214 Uw
Ecdyonurus affinis Eaton 196,321 no consensus
E. angelieri Thomas 203,339,340 Uw
E. aurantiacus (Burmeister) (= *E. fluminum*) 196,260,321 Us
E. carpathicus Sowa 321 Uw
E. dispar (Curtis) 143,162,196,234,321,323,368 Us
E. fasciocolatus Sowa 321 Us
E. forcipula (Pictet) 180,196 Uw
E. insignis (Eaton) 143,196,200,321,323 Us
E. joernensis Bengtsson 355
E. kibunensis Imanishi 352
E. lateralis (Curtis) (= *Heptagenia lateralis*) 139,143,164,178,196,228,231,310,
321,323 Uw
E. macani Thomas and Sowa 321 Uw
E. picteti Meyer-Dür. 159,196 Uw
E. quadrilineatus Landa 196,198,321 Uw
E. starmachi Sowa 321 Uw
E. subalpinus Klapalek 180,196,321 no consensus
E. submontanus Landa 196,198,321 Us
E. tobironis Takahashi 218
E. torrentis Kimmins 121,138,143,196,321,323,368 Uw
E. venosus (Fabricius) 99,103,117,143,164,180,196,231,260,303,321,339,340,368
see text
E. yoshidae Takahashi 125,352 Uw
Epeorus sp. 31,51,137,191,208 no consensus
E. aesculus Ueno 218,337
E. albertae McDunnough 90,204
E. deceptivus (McDunnough) 90,204,301 Uw
E. fragilis (Morgan) 241,254
E. ikanonis Takahashi 125,277 Uw
E. latifolium Ueno 125,218,277,352 MBws
E. longimanus (Eaton) 90,148,179,204,301,371 Uw
E. maculatus Tshernova 218

- E. pleuralis* (Banks) 241,251 Uw
E. rubidus (Traver) 51
E. sylvicola Pictet (= *E. assimilis*) 180,196,260,321,323 Uw
E. torrentium Eaton 339,340 MBws
E. uenoi Matsomura 125,277,352 no consensus
E. vitreus (Walker) 107,171,217,254,299 Uw
Heptagenia abnormis Tshernova 218
H. aphrodite McDunnough 51,140
H. arsenjivi Tshernova 218
H. coeruleans Rostock 196,321 Uw
H. dalecarlica Bengtsson 354,355 Uw-2Y
H. diabasia Burks 107 Us-Uw
H. elegantula (Eaton) 93
H. flava Rostock 178,196,218,321 Uw
H. flavescens (Walsh) 56,107,289 Uw
H. fuscogrisea (Retzius) 19,41,143,153,178,196,355 Uw
H. hebe McDunnough 107,217 Us-Uw
H. inconspicua McDunnough 289
H. junno McDunnough 299
H. kibunensis Imanishi 218
H. longicauda (Stephens) 143,321 Uw
H. lucidipennis (Clemens) 56,107,226 Us
H. maculipennis Walsh 56,289
H. pulla (Clemens) 56,107,140,171,217
H. soldatova Tshernova 218
H. sulphurea (Müller) 143,178,196,200,201, 231,321,323,354,355 see text
H. umbricata McDunnough 289
H. yoshidae Takahashi 218
Ironodes nitidus (Eaton) 93,191,204 Uw
Macdunnoa nipawinia Lehmkuhl 212 Us
Pseudiron centralis McDunnough 208 Us
Rhithrogena sp. 137,191,218 Uw
R. alpestris Eaton 196 Us
R. amica Traver 299
R. brunnea (Hagen) 122
R. diaphana Navas 196,273,321,323 Us
R. ferruginea Navas 321,323 Uw
R. germanica Eaton (= *R. haarupi*) 143,196,321,323,368, Uw
R. gorganica Klapalek 321 Uw
R. hageni Eaton 301 Uw
R. hercynia Landa 196,198,321,323 Uw
R. hybrida Eaton 196,321 Uw
R. impersonata (McDunnough) 107,217 Uw
R. iridina iridina Kolenati 321 Us-Uw
R. iridina picteti Sowa 339,340 MBws
R. japonica Ueno 125,277 Uw

- R. jejuna* Eaton 56,107,217 Uw
R. loyale Navas 196,321,341 no consensus
R. minus Eaton 267
R. morrisoni (Banks) 206 Uw
R. pellucida Daggy 107,217 Us
R. sanguinea Ide 217
R. semicolorata (Curtis) 13,46,96,103,117,121,138,180,196,228,229,231, 321,323,
 330,339,340,368 see text
R. undulata (Banks) 107 Uw
R. unicolor Tshernova 218 Uw
R. virilis McDunnough 148,371 Uw
Spinadis sp. 107
S. wallacei Edmunds and Jensen 92
Stenacron interpunctatum canadense (Walker) 32,56,69,102,107 Uw
S. interpunctatum frontale (Banks) 27,140,217
S. interpunctatum heterotarsale (McDunnough) 140,217,299
S. interpunctatum (Say) (+*S. interpunctatum interpunctatum*) 51,55,107,
 137,217,226,
 244,284,289,370
 see text
Stenonema sp. 51
S. bipunctatum (McDunnough) 107,140 Uw
S. exiguum Traver 27,107,284 no consensus
S. femoratum (Say) 226,289 MP
S. fuscum (Clemens) 107,140,217 Uw
S. integrum (McDunnough) 51,107,217 Uw
S. ithaca (Clemens and Leonard) 217
S. luteum (Clemens) 56,217
S. mediopunctatum (McDunnough) 107 Uw
S. nepotellum McDunnough 140,217
S. pudicum (Hagen) 51
S. pulchellum (Walsh) 107,217 Uw
S. rubromaculatum (Clemens) 56,289
S. rubrum (McDunnough) 107,140,217 Uw
S. smithae Traver 27,284 MNP
S. terminatum (Walsh) 107 Uw
S. tripunctatum (Banks) 55,56,107,171,217,226,305 see text
S. vicarium (Walker) 69,70,217,305 Uw
Thalerosphyrus sp. 31 MNP

Leptophlebiidae

- Adenophlebiodes decoratus* Kimmins 347 MNP
Atalophlebiodes sp. (= *Deleatidium*) 366,367 Uw-MBws
Calliarcys humilus Eaton 85,286
Choroterpes sp. 31,144,145 MNP

- C. albiannulata* McDunnough 208 Us
C. basalis (Banks) 57,226 Us
C. bugandensis (Kimmins) 347 MNP
C. crocatus Allen 1
C. curtis (Kimmins) 347,348 MNP
C. elegans (Barnard) 286
C. hubbelli Berner 27
C. mexicanus Allen 1,245 MP
C. nigrescens Barnard 286
C. picteti (Eaton) 127,196,321 Us
C. trifurcata Ueno 125 MBws
Cryptopenella facialis Gillies 119,286
Dipterophlebiodes sp. 31 MNP
Gilliesia hindustanica (Gillies) 119,286
Habrophlebia sp. 51
H. fusca (Curtis) 117,193,194,196,231,310 Uw
H. lauta McLauchlan 97,117,193,194,196,228,260,294,295,296,310,321,323,339,
340 Uw
H. vibrans Needham 51
Habrophlebiodes sp. 31 MNP
H. americana (Banks) 51
H. brunneipennis Berner 27
H. gilliese Peters 286
H. prominens Ulmer 285,286,356
Habroleptoides sp. 31,286
H. modesta (Hagen) 117,129,196,260,294,295,296,314,321,323,339,340 Uw
Isca purpurea Gillies 119,286
Leptophlebia austrina (Traver) 51
L. cupida (Say) 29,32,57,60,62,64,67,68,69,137,141,142,150,151,152,169,
170,217,226,237,254,255,264,289,325,336,349 Uw
L. intermedia (Traver) 27
L. marginata (L.) 19,39,41,43,44,45,128,143,178,184,196,221,230,231,258,278,
289,319,342,355 Uw
L. nebulosa (Walker) 57,217
L. pacifica (McDunnough) 209 M?
L. vespertina (L.) 23,39,41,43,44,45,143,153,178,186,187,196,231,253,258,278,319,
321,355 Uw
Paraleptophlebia sp. 51,154
P. adoptiva (McDunnough) 74,123,172,217,299 Uw
P. bicornuta (McDunnough) 191,215 Us
P. bradleyi (Needham) 27
P. chocolata Imanishi 125,218 no consensus
P. cincta (Retzius) 143,178,196,310,321 no consensus
P. debilis (Walker) 32,60,123,137,191,215,217,328 see text
P. gregalis (Eaton) 191
P. guttata McDunnough 51,123,289,299

- P. heteronea* (McDunnough) 191
P. lunata Tshernova 218
P. moerens (McDunnough) 69,123,250 Uw
P. mollis (Eaton) 69,73,74,123,172,190,217 Uw
P. praepedita (Eaton) 32,57,217,254
P. spinosa Ueno 125,352 U?
P. stradii Eaton 128,355
P. strigula (McDunnough) 217
P. submarginata (Stephens) 103,129,143,178,196,203, 228,231,260,321,339,340 Uw
P. temporalis (McDunnough) 215 Uw
P. volitans (McDunnough) 27,172,284 MNP
P. wernerii Ulmer 178,196 Us
Simothraululus seminiger Ulmer 286,356
Thraulodes sp. 28 MNP
Thraululus sp. 31
T. bellus Eaton 85,286,358
T. fasciatus (Kimmins) 286,287,347
T. torrentis (Gillies) 286,287
Traverella sp. 93
T. albertana (McDunnough) 28,208 Us

Metretopodidae

- Metretopus* sp. 355 Uw
M. borealis Eaton 93,128,178
Siphloplecton basale (Walker) 32,57,63,137,152,217,226 Uw
S. speciosum Traver 27,284

Neoephemeridae

- Neoephemera* sp. 27
N. bicolor McDunnough 28
N. purpurea (Traver) 28
N. youngi Berner 284
Neoephemeropsis sp. 31

Oligoneuriidae

- Elassoneuria insulicola* Demoulin 302 Uw
Homooneuria dolani Edmunds, Berner and Traver 93
Lachlania sp. 93 Us
L. dencyanna Koss 189
L. powelli Edmunds 86
L. saskatchewanensis Ide 208 Us
Oligoneuriella baskale Soldan and Landa 318 Us
O. mikulskii Sowa 321 Us
O. mongolica Soldan and Landa 318 Us
O. pallida Hagen 321 Us
O. rhenana (Imhoff) 196,292,293,321,323 Us

O. zanga Soldan and Landa 318 Us

Polymitarciidae

Ephoron album (Say) 38,93,94,192,208,243,289 Us

E. leukon Williamson 169 Uw

E. virgo (Oliver) 196,218,321 no consensus

Povilla adusta Navas 30,71,72,146,147,291,347 MNP

Tortopus incertus (Traver) 27,28,243,315 2Y

Potamanthidae

Potamanthodes sp. 31

Potamanthus sp. 222

P. distinctus Traver 243,289

P. luteus (L.) 196,218,276,321 Uw

P. myops (Walsh) 15,243,289 2Y

Prosopistomatidae

Prosopistoma africanum Gillies 130

P. oronti Alouf 9 Uw

Siphonuridae

Ameletus sp. 51,235 Uw

A. celeroides McDunnough 26 Uw

A. connectina McDunnough 191

A. costalis Matsumura 125,352 U?

A. inopinatus Eaton 10,41,43,44,48,97,120,121,143,180,184,196,202,231,321,354,355
Uw

A. ludens Needham 59,336 Uw

A. montanus Imanishi 125,218 U?

A. oregonensis Eaton 32

A. similior McDunnough 93

A. sparsatus McDunnough 137 Uw

A. validus McDunnough 93

A. vancouverensis McDunnough 191

A. velox Dodds 26 Uw

Aneletris eximia Edmunds 211 Us

Coloburiscus humeralis (Walker) 369 Uw

Edmundsius agilis Day 28,93

Isonychia sp. 31,284

I. bicolor (Walker) 57,58,217,254,289,335,336 MBws

I. harperi Traver 217

I. pictipes Traver 27 MNP

I. sadleri Traver 217,299

I. sicca (Walsh) 208 Us

I. thalia Traver 51

Nesameletus sp. 367

- Oniscigaster wakefieldi* McLachlan 247,248 Uw
Parameletus sp. 355
P. columbiae McDunnough 87,93 Us
P. minor Bengtsson 218
Siphonisca aerodromia Needham 28,93 Us
Siphonurus aestivalis (Eaton) 8,35,43,44,153,178,196,197,355 Us-MBss
S. alternatus (Say) (not including *S. linnaeanus*) 16,32,60,137,140,217 Us
S. armatus (Eaton) 131,143,196,197 Us
S. lacustris (Eaton) 36,41,43,44,45,83,131,143, 164,196,197,231,321,353,355 see text
S. linnaeanus (Eaton) 128,143,153,178,196,197,355 Us
S. marshalli Traver 289
S. mirus Eaton 51
S. occidentalis Eaton 191,209 Uw
S. quebecensis (Provancher) 217
S. rapidus McDunnough 217
S. zetterstedti Bengtsson 218

Tricorythidae

- Tricorythodes* sp. 152 Us
T. albilineatus Berner 27,284 MNP
T. allectus Needham 57,226,254
T. atratus McDunnough 133,134,289,336 Us/MBss
T. explicatus (Eaton) 217
T. fictus Traver 238
T. minutus Traver 16,93,274,275,306 no consensus
T. stygiatus McDunnough 217
Tricorythus maculatus Kimmins 347 MNP
T. tinctus Kimmins 347 MNP

